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# COMMENTS ON SOME MEDITERRANEAN ROCKDWELLING HELICIDS

J. F. M. DE BARTOLOMÉ\*

(Presidential Address, delivered 11 March 1981)



*Abstract:* Species have been defined as 'groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups'. If this is adopted, it is suggested that many generally accepted named species with widely differing shell characters are not species but 'forms', 'local races' or 'varieties'.

The more conspicuous divergent but interbreeding mediterranean forms are considered, with early and modern authors' comments thereon and the efforts of some of them to adapt the nomenclatural system so as to indicate the close relationship between such forms.

## INTRODUCTION

My address in March 1980 dealt with the very variable species *Marmorana* (*M.*) *serpentina* (Férussac), and tried to find other local races to be added to those described by K. L. Pfeiffer (1931). The forms in that species were only distinguished by trivial features that might be called decorative. For example, the amount and location of brown colouring around the aperture: none in *carae* Cantraine; a fleck on the columella in *isarae* Paulucci; more in others and the maximum with *isilensis* Villa. The marbling too, which usually obliterates the banding, varied from blotches to a delicate arabesque.

Today I shall comment on variations that might be called structural, such as keels and umbilicuses, with lips getting a mention. Instead of one species, I shall refer to number in a dozen or so genera, and instead of two islands and a couple of bits of mainland I shall wander from Tetuan to Turkey and from the Alps to the Atlas and the Siwa depression in Egypt but it is limestone most of the way. Loosely speaking, the predominant shape in the genera concerned is more or less globose with a rounded periphery, and smooth or only gently reticulate or granulate surface. The umbilicus is closed in the adult. Today I shall be looking at the exceptions, that is the depressed strongly keeled and rugose forms and those with a wide open umbilicus. As it is to be expected, many of these highly specialized forms tend to have a narrow geographical distribution, being restricted even to a single locality or series of disjointed localities, with the more tolerant and dominant globose forms closely surrounding them.

## KEELED VARIANTS

The supreme keeled form *Iberus gualtierianus* (L.) – which is correctly spelled with two 'i's – has a disjointed distribution as isolated colonies on the coastal mountains of southern Spain from Valencia to Cadiz. It is strongly keeled, depressed to the point on occasions of being concave above, and very rugosely decussate – a Sheffield file-maker, using a term of art, said that it had a surface like a 'bastard file'. Widespread around it is the globose and weakly decussate *alonensis* Férussac which, if the form *alvaradoi* García San Nicolás is included, is

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found, also in colonies, from Cadiz to the Pyrenees and inland as far as Madrid and Zaragoza. The greatest concentration of *gualtierianus* seems to be in the area between Granada, Almeria and Motril. It is absent in the adjoining province of Malaga, but 100 km west of Granada on the limestone block of El Torcal near Antequera (Malaga province) form *rositai* Fez has its solitary locality, though the form was named on one dead shell found 70 km further south-west at Benaoján near Ronda, where four days hunting by me produced nothing like it. Smaller than *gualtierianus*, its much finer spiral lines hardly cut the strong radial ribs. It is restricted to the scarcely man-wide passages and narrower cracks of the fantastically carved wilderness of stone of El Torcal Alto, while on the lower parts of the block and at the foot of the cliffs surrounding it form *loxanus* Rossmässler, a bit like a smaller and depressed *alonensis*, is common. Only 15 km west of El Torcal, there is another isolated form, *cobosi* Ibañez & Alonso. Found on the south-facing cliff of the block of Sierra del Valle de Abdalajis, it is rather like a miniature *gualtierianus* the exerted keel of the upper whorls often giving it a pagoda-like appearance. On the more broken eastern cliffs of the block, just north of the village, I found the widespread form *marmoratus* Férussac, the smallest rounded *Iberus*, depressly globose and delicately decussate.

Across the straits in Morocco in the mountains between Ceuta and Tetuan, *Rossmassleria* has three keeled forms (including *subscabriuscula* Bourguignat) which look similar to me, and are perhaps local races. Just across the valley from Tetuan on the Beni Hosemar mountains three rounded forms are found, which Kobelt named *tetuanensis* (with a variety *boettgeri*), *sicanoides* and *weberi*, and which are just distinguishable; a fourth, *scherzeri* Zelbor, is found on Gibraltar. All look near to sicilian *Murella*. Further south, in the Atlas mountains, *Tingitana*, a subgenus of *Alabastrina*, has a keeled form *minettei* Pallary (which looks more like an *Iberus*) and others. There are many unkeeled adult forms.

Sicily has the other large concentration of keeled forms, but I will mention first four minor occurrences.

*Tyrrheniberus* from eastern Sardinia has only three species: *ridens* Martens, compactly globose; *villicus* Paulucci, roundly depressed and openly umbilicate (both species with spiral lines); and *sardonius* Martens, keeled, depressed and umbilicate, without spiral lines but with strong radial ribbing.

*Macularia* has only two species: *niciensis* Férussac, rounded and globose and widespread from Nice eastwards into Italy, and *saintyvesi* Caziot from the permanently damp silicious Permian rocks in the Gorges de Cians, some 50 km northwest of Nice, where other odd forms occur. It is depressed, bluntly keeled, thin, fragile and with something of the reddish colour of the rocks. However, as immediately north of the narrow gorge I found specimens as rounded and globose as *niciensis* but with a bit of the rock colour of *saintyvesi*, I am doubtful as to its status.

In Egypt, in addition to *desertorum* Forskal and *ehrenbergi* Roth and other rounded globose forms near to them, *Eremina* has a keeled form, *zitteli* Boettger, connected to *ehrenbergi* by intermediate forms. It is found in the Siwa oasis on the Libyan border and northwards to Mersah Matruh. It has a marked resemblance to *gualtierianus*.

Alone among its subgenera, the part of *Levantina* called *Gyrostomella* has a keeled form, *leachi* Férussac, not depressed but swollenly lenticular and strongly ribbed. The one other species is rounded and globose. Both seem rare and come from the mountains near Tripoli in western Libya.

Most of Sicily is the domain of that tough and tolerant thing *Marmorana* (*Murella*) *muralis* (Müller). It is absent from the Madonie mountains on the north coast and thence from Palermo to Marsala, in which area it is replaced by an assortment of rounded globose forms and a smaller number of depressed keeled ones. The diversity may be due to the coastal mountains having been islands or barely connected peninsulas during the Pleistocene, producing an island-type fauna.



The northwestern tip of Sicily, Capo San Vito, where the sea and winds always dance, produces the form *bulowi* Maltzan: conical, sharply keeled and strongly ribbed above, with spiral lines producing a fine granulation. Higher up on Monte Monaco at the tip of the cape I found a rounded, depressly globose form near to *ascherae* Kobelt, which is found on Monte Erice near Trapani. On the next mountain at the base of the cape Pfeiffer (1931) found *conspicua* Benoit, and between there and Monte Erice forms *excelsa* K. L. Pfeiffer and *iparia* Benoit occur. Authors relate these forms variously to *globularis* Philippi and *platychela* Menke, both rounded globose forms from the mountains nearer to and surrounding Palermo.

Eryx, Monte Erice (formerly called Monte San Giuliano as the Norman Count Roger had a vision of St Julian there while besieging it in 1080) is dominated by the keeled *scabriuscula* Deshayes, while *ascherae* has a small corner I have not yet found. The form called *scabriuscula* is low conic above, with a sharp keel exerted over the next whorl to give a pagoda-like effect. Inland a little south of east there are isolated colonies at Alcamo, Segesta and Calatafimi, which Benoit called Calatafimini. Further inland I found a colony at Corleone. These inland forms lose the exerted keel and are the form *paciniana* Philippi. The striae vary in intensity and the occasional marking of reddish brown dots pales or is absent. The Corleone form is however darker. Just south of Trapani comes the isolated colony of *drepanensis* Huet, small and often pagoda-like. All these are forms of *scabriuscula* but curiously there are few rounded globose forms living near them. The coastal region from Marsala to Sciacca produces only colonies of very rugose *muralis*.

The Romans called Sciacca the 'Baths of Selinus' although the ruins of Greek Selinus are 20 km to the west. Monte Calogero at Sciacca thus houses form *selinuntina* Philippi, conical with an unexserted keel but well marked bands. Other hardly distinguishable varieties have been named of course. The cliffs of Rocca Nadore, clearly seen from Monte Calogero, have *nadorrica* Westerlund; as its keel is often exerted I link it with *scabriuscula*, though Westerlund and Kobelt link it with *bulowi*. Pfeiffer (1931) links them all with *scabriuscula*. Here, just up the road from Caltabellotta, the rounded globose *caltabellottensis* Kobelt occurs. Its dark darkening of irregular blotches must tie it up with *ascherae* and its kin from Capo San Vito and Monte Erice.

#### UMBILICATE VARIANTS

Leaving keels for a while to look into some umbilicuses, I must say that I am not concerned with the many cases where the adult has just failed to close the umbilicus of the pre-adult shell, leaving a mere chink. Many such forms have been given varietal names but the situation seems to be most common with the depressed, widely coiled specimens which, I guess, just ran out of material for covering the inevitably wider hole.

In *Iberus*, the somewhat funnel-shaped umbilicus of the form *gualtierianus umbilicatus* Kobelt may indicate a regular local form. Plainly related to *alonensis*, the forms *campesinus* Ezquerro and its allies, and *lorcanus* Rossmässler, are not only openly umbilicate but also have a remarkably broadened lip, often continuous and detached at its base. The smaller *guiraoanus* Rossmässler, which is depressed and unkeeled, is openly umbilicate. These are all from the Almeria-Granada-Malaga region.

*Levantina* (*Assyriella*) *escheriana* (Mousson) has an open umbilicus and a broad lip detached at its base. *L. (A.) ninivita* (Galland), too, has an open umbilicus but a normal lip. *L. (A.) mardinensis* (Kobelt) is normal in both respects. All three come from near Mardin and Cizre, along both sides of the border of Turkey with Syria and Iraq. *L. (L.) spiriplana* (Olivier) from Rhodes produces a few specimens with a chink but the larger depressed *L. (L.) hierosolyma* (Boisier) is openly umbilicate. The less depressed *L. (L.) caesareana* (Parreys) and its higher spired variety *wernerii* Rolle are not. In passing I would mention that in conversation with H.



E. J. Biggs he expressed some doubts as to how distinct those three species really were. However Heller (1979) describes the clear, if zigzag, boundary line between the areas in Israel that these large forms occupy. It runs from near Qumran at the north end of the Dead Sea, passing north of Jerusalem roughly in the direction of Tel Aviv. *L. caesareana* is found north of the line, with *weneri* at its western end and *hierosolyma* south of it. I would mention that while at St Peter's church at Antioch (today called Antakia) in southern Turkey and north of the line, I found, as expected, a form close to *caesareana*, while much further north at Datça on the Marmaris peninsula in western Turkey, in sight of Rhodes, I found two openly umbilicate specimens which I should call *hierosolyma*.

With these facts and observations, I will look at what some authors, ancient and modern, have made of the complexities.

#### EARLIER AUTHORS' COMMENTS

In 1876 Kobelt in his introduction to volume 4 of Rossmässler's *Iconographie*, the first he edited, stated his view on the 'species concept'. 'What I can always distinguish from all other forms, that is a good species, but where I have first of all to make a thorough comparative study, or need a reliable statement of the localities in order to tell two kinds apart, then simply they are not species'. That perhaps was the first shot in his war with Bourguignat. Two or three years later he travelled in Sicily from Trapani to Palermo and observed by the wayside the chain of intermediate forms linking the keeled and depressed *scabriuscula* from Monte Erice, with the rounded and globose *sicana* Férussac from Monte Pellegrino at Palermo (Kobelt 1879, 1881).

In 1891 Schuberth and in 1908 Wiegmann and Hesse dealt with the anatomy of most of the keeled and unkeeled west sicilian *Murella*, finding no constant material differences between them. There were variations in the dimensions of the genitalia, but the ranges nearly always overlapped.

In 1913 Boettger found a similar lack of distinction between the anatomy of the then known forms of *Iberus* (Rossmässler's *carthaginiensis* and *loxanus* perhaps excepted) and again was able to show shell forms linking not only keeled *gualtierianus* with rounded globose *alonensis* but all the forms.

In 1929 Rensch collected in western Sicily, followed a year later by K. L. Pfeiffer who published his results in 1931, treating 32 named forms as varieties of *muralis*, *scabriuscula*, *globularis* or *platychela*. Rensch did not publish until 1937 and then based himself on his own findings, Pfeiffer's and Kobelt's. Apart from confirming the linking of all the forms, he tried to see if the keeled and roughly striate forms could be connected with a hot dry climate. They are more numerous in the mediterranean region than in the damper and cooler north. The rounded globose forms in Sicily mainly live high up in the cooler coastal mountains, but this does not apply to *Iberus* in Spain, where the keeled forms are restricted to the coastal mountains while globose *alonensis* extends far inland.

H. E. J. Biggs was in Egypt from 1937 to 1942 and studied the forms of *Eremina* (Biggs 1959). Having linked *desertorum* with *ehrenbergi*, he joined them to the other forms, including the keeled *zitteli*, in his 'catenation'. He discusses their environment but does not suggest any differences likely to lead to variations in shell.

Heller (1979) dealing with his borderline between the umbilicate *hierosolyma* and the form *caesareana* says that it shows no association with altitude, rainfall, temperature, climatic zones, phytogeography, or the distribution of predators. Moreover, examination of shells found at prehistoric sites dating back 50,000 years shows only the form found living nearby today. He admits that a narrow hybrid zone occurs in most places along the borderline.



Although when far from the line *caesareana* resembles *hierosolyma* in shell height and general shape, he found that when approaching the line the high-spined *wernerii* replaces typical *caesareana* and so diverges from *hierosolyma*.

García San Nicolás (1957) gave a wealth of information regarding *Iberus* and the anatomy and shells of the various forms but, localities apart, does not indicate any great distinction in the respective environments for *gualtierianus* and *alonensis/alvaradoi*. She does however disagree with Boettger's treatment of all forms as varieties of *gualtierianus*, though admitting that intermediate forms may occur in nature.

Whatever the undiscovered factor may be that led to the evolution of the depressed keeled forms and the broad-lipped ones, it seems to me that the former would have the better chance of retiring from the heat into deeper cracks in the rock and packing themselves together more tightly (as they do) and the latter of gluing themselves more firmly to rock surfaces (as many still do).

#### EXPERIMENTAL INTERBREEDING

Although the existence of intermediate forms or hybrids in nature seems quite plain, some confirmation has been obtained by experimental breeding.

Rensch (1937) describes, in addition to five breedings between specimens of the same form, two crosses between distinct forms: *Murella globularis* with *connexa* (both rounded), and the rounded *sicana* with the keeled *segestana* Philippi (a variety of *scabriuscula*). Furthermore, and horror or horrors, he raised offspring from a cross between *Murella platychela* from Palermo and *Ambigua surrentina* (A. Schmidt) from Sorrento. Most died young but a few reached full size from this inter-subgeneric cross.

In 1938 Biggs successfully crossed *Eremina desertorum* with *ehrenbergi* in Egypt (Biggs 1959). Both are rounded forms. The last surviving offspring died in England aged four years and a quarter, but as no dart was found it was apparently not yet adult. Anatomically, he says, it was 'perhaps a little more like *desertorum*'. He does not describe the shell.

In 1955 García San Nicolás crossed *Iberus gualtierianus* with *alonensis*. Slightly amplifying Biggs' comment in 1959, eleven offspring resulted which she studied and from which she selected one for the description of the shell which she gave in her paper. They were then, in October 1956, aged 18 months and not yet adult. In a letter this year (1981) she confirms that in the spring of 1957 they appeared sexually mature, bred normally and that various batches of eggs were laid. The first generation offspring and those later derived from them have forms similar to the numerous *Iberus gualtierianus-intermedius* described by Boettger and others, which her paper mentions.

In 1975-77 Heller successfully crossed *Levantina caesareana* with *hierosolyma* and the offspring backcrossed with the parent forms and bred among themselves (Heller 1979). The offspring show little variation from specimens in the hybrid zone. However the crosses between the parent forms and the backcrosses between hybrid and parent were far more successful than the crosses between the hybrids, which suggests that later generations of hybrids are at a disadvantage. Both Biggs' and Heller's observations show that an individual will prefer to mate with its own kind, even if another is waiting nearby and willing.

While I do not think it is possible to come now to any firm conclusions regarding this multiplicity of interbreeding forms within a genus, or the conspicuous parallels of variation within distinct genera, one warning and one problem need a mention.

Rensch points out that given only dead shells or fossils of the keeled forms *Murella scabriuscula*, *Tyrrheniberus sardonius* and *Rossmassleria subscabriuscula* one would hardly hesitate to put them together in one genus or race group, and the unkeeled *Murella platychela*, *Tyrrheniberus villicus* and *Rossmassleria tetuanensis* (Kobelt) in another. This, he points out, is a



warning that the conclusions of palaeontological taxonomy are at times much more hypothetical than the most prudent worker would like to believe. I wonder if cladisticians would fare better.

## NOMENCLATURE

The problem is simply 'what is a species?', with the consequential question 'what form of nomenclature is appropriate for these interbreeding forms?'. Kobelt's view I have quoted and later he wrote more strongly. Of the sicilian *Murella* he wrote (1881) that they are 'one species which plainly makes a mock of our present species concept'. Nevertheless he continued to refer to the forms by separate specific names and added a few new ones, and did not treat them all as *muralis* Müller, the oldest name. On the other hand Boettger (1913) did name all the forms of *Iberus* as forms of *gualtierianus*, e.g. *Iberus gualtierianus alonensis*. In 1931 Pfeiffer, as before mentioned, put the *Murella* forms into four species, e.g. *Murella scabriuscula bulowi* or *M. platychela sicana*. Rensch (1937) treats them all as forms of *muralis*, e.g. *Murella muralis muralis* or *M. muralis scabriuscula*. However García San Nicolás (1957), Biggs (1959) and Heller (1979) are unmoved by their own results and say *Iberus alonensis*, *Eremina ehrenbergi* and *Levantina hierosolyma* respectively. At any rate for labels on boxes I agree with them. I am not very fond of that perhaps mythical bird, the thrushiest thrushier thrush, but to indicate the closer relationships in, say, *Marmorana*, it might be necessary to use '*Marmorana (Murella) muralis scabriuscula paciniana* (Philippi)', which is scarcely practical.

As some sort of conclusion, I would apply to all the genera I have mentioned Biggs' words regarding *Eremina*: 'we are not dealing with a static genus but a group of snails which is plastic, actively evolving here and now'. As for their future, may the fittest long survive, but I do not think they will be the most attractive—the keeled ones.

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# THE STATUS OF *LITTORINA AESTUARII* JEFFREYS AN APPROACH USING MORPHOLOGY AND BIOCHEMICAL GENETICS

J. MOYSE,\* J. P. THORPE\*† and E. AL-HAMADANI\*

(Accepted for publication 13 December 1980)

**Abstract:** As a contribution towards rationalizing the taxonomy of the genus *Littorina* and to demonstrate the use of the technique of enzyme electrophoresis in molluscan taxonomy, a reassessment was made of *Littorina aestuarii* Jeffreys 1869. Certain morphological features of specimens from the type locality showed strong differences from *L. mariaae* but their distinction from *L. obtusata* was less marked. Enzyme studies corroborated these findings and demonstrated that *L. aestuarii* is genetically similar to, and therefore should be regarded, we suggest, as a junior synonym of *L. obtusata*.

## INTRODUCTION

In the course of comparative studies on the reproductive strategies of the fucoid-grazing rocky-shore gastropods *Littorina obtusata* (L.) and *L. mariaae* Sacchi and Rastelli, it became apparent that there were unresolved taxonomic questions. The status of the northern form, sometimes known as *L. palliata* Say (see Thorson 1941) which has been regarded as conspecific with *L. obtusata* (see Colman 1932) is to be the subject of a further paper by us (Moyse *et al.*, in preparation). The present paper attempts to re-evaluate the status of *L. aestuarii* Jeffreys 1869, a rare form from creeks in South East England.

Following Jeffreys' description (1869) subsequent writers either accept the specific status of *L. aestuarii* (e.g. Gordon 1910, Doughty 1934, S. M. Smith 1974) or attempt to equate it with *L. palliata* (Dautzenburg and Fischer 1915). With the recognition of *L. mariaae* Sacchi and Rastelli (1966), as a species separate from *L. obtusata* the possibility that *L. aestuarii* might be equated with *L. mariaae* must be examined, since their published descriptions bear certain superficial similarities and especially in view of the frequently abundant occurrence of the latter in estuaries. This equation has already been proposed by S. M. Smith (1978). Populations of *L. aestuarii* have been reported from brackish sea-lochs in the Outer Hebrides (Waterston, pers. comm.) but these cannot usefully be considered until the validity of the species at the type locality has been confirmed.

In re-examining the taxonomic status of *L. aestuarii* this paper re-assesses the morphological evidence and presents the results of a comparative study of some isoenzymes of this form, *L. obtusata* and *L. mariaae*.

For the taxonomist the technique of enzyme electrophoresis has considerable potential (Avisé 1974, Thorpe 1979). Its main advantage is that it enables individuals to be assigned, generally with a high level of statistical probability, to one or another gene pool of interbreeding or potentially interbreeding animals.

Clearly, individuals not belonging to at least potentially interbreeding gene pools cannot

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by any definition be of the same species, whilst conversely those showing little genetic differentiation are unlikely to be of different species. There is now available a considerable body of published data from a wide variety of animal and plant species, which shows that, on average, individual organisms from allopatric populations of a single species show genetic differences at only a small proportion (generally less than 10%) of gene loci. Interspecific comparisons usually show far greater levels of genetic differentiation (typically about 50%). Further information on genetic variation between taxa is given by Avise *et al.* (1975) and Thorpe (1979).

Biochemical taxonomy based upon studies of enzyme variation has several additional advantages over the more conventional methods. Conclusions may be less open to individual interpretation and subsequent dispute than those based on morphological criteria and often results can be obtained with greater rapidity. In some circumstances isoenzyme analysis is almost the only practicable technique presently available. This is particularly true for the identification of cryptic species (see for example Manwell and Baker 1963, Miller and El Tawil 1974, Steiner *et al.* 1977, Thorpe *et al.* 1978). It is also true in cases such as that presented here in which there is doubt as to which of two 'species' a morphologically intermediate type may belong (see also Thorpe *et al.* 1978, Maturo and Thorpe 1979, Mundy and Thorpe 1979, 1980, Thorpe and Mundy 1980).

## METHODS

*Field Survey.* An accurately identifiable location description given by Jeffreys (1869, p. 205) for *L. aestuarii* represents a valid type locality. He states, 'on the banks of the river Deben at Shottisham Creek near Sutton, (Suffolk, England), and at Manningtree'. Shells from these localities are preserved in the Jeffreys collection in Washington (Warén 1980, p. 21). The reference to Manningtree can be disregarded for definitive purpose since the Shottisham Creek reference is valid and takes priority. This site (Fig. 1) was visited by J. Moyse in September 1978. Changes have occurred in the century since the original record; the sea wall has been largely rebuilt and the Shottisham Creek now drains into the Deben at a more southerly point. *Spartina* sp. now forms a high level sward with steep crumbling banks. A few patches of *Fucus vesiculosus* are to be found on occasional boulders and on the lower parts of the sea wall between gaps in the *Spartina* marsh. These *Fucus* patches are affected by deposited river scum and stranded salt-marsh debris, giving them a generally dirty texture. Careful search amongst this weed in September 1978 revealed just five specimens of live *Littorina* feeding there. These appear to be similar to those seen by Jeffreys so we refer to them as *L. aestuarii*. Some egg masses were also observed on the *Fucus* but were not collected. A few *L. saxatilis* agg. were also seen in the locality but no other *Littorina* species.

Several other points on the banks of the Deben between the open coast and Woodbridge were visited in 1978 but no *L. aestuarii* were observed even where *Fucus* occurred; only two substantial *Littorina* populations were found and sampled. The first of these was at the mouth of the estuary at Bawdsey Manor (see map Fig. 1), where a population of typical *L. obtusata* was found in mid-littoral *Fucus vesiculosus* and *Ascophyllum nodosum* growing on stones. The second was a population of *L. mariae* found on the upper half of the shore on a patch of *Fucus vesiculosus* growing on shaley stones at Stonner Point. This population was monomorphic – all specimens having 'dark reticulate' shells.

*Morphological Methods.* The three field samples were kept alive in circulating seawater in the Marine Science Laboratory of the University College of Swansea for several months prior to analysis.

In addition to the five specimens of *L. aestuarii*, six specimens each of the populations of *L. mariae* and *L. obtusata* from the River Deben were selected for enzyme analysis. Morphological features of these seventeen specimens were analysed immediately prior to the enzyme analysis. The remaining specimens of *L. obtusata* and *L. mariae* were



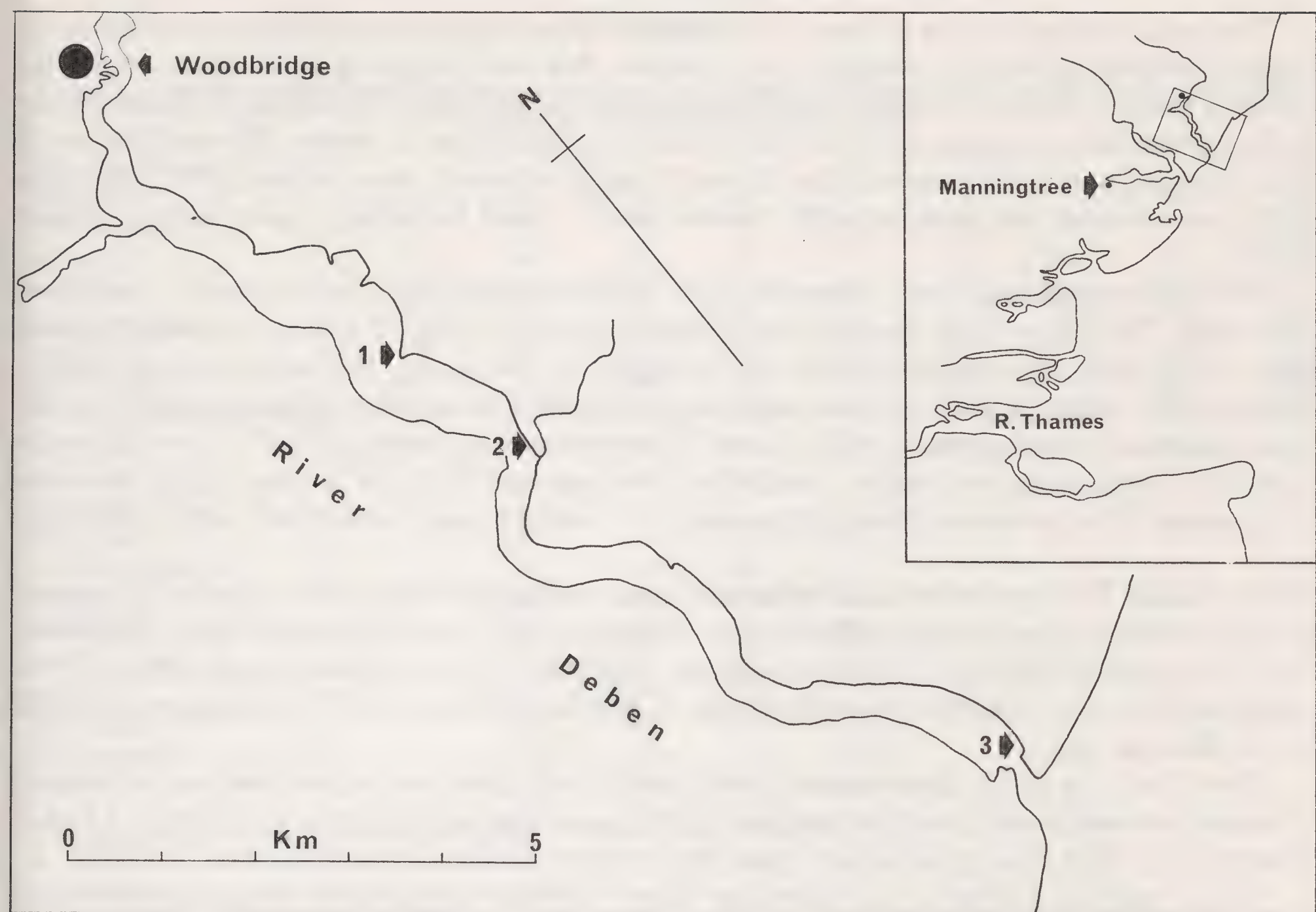


Fig. 1. Principal sampling points: 1, Stonner Point; 2, Shottisham Creek; 3, Bawdsey Manor.

examined by the same standard morphological methods. These included measuring shell height, shell aperture and in particular shell spire angle. Soft part features, particularly of the penis were recorded.

**Electrophoresis Methods:** Electrophoresis was carried out using  $180 \times 150 \times 6$  mm horizontal starch gels made from  $12\frac{1}{2}\%$  hydrolysed starch (Connought Diagnostics, Willowdale, Ontario), on Shandon electrophoresis apparatus (Model U77 (after Kohn) SAE 3225). Live specimens were prepared for electrophoresis by removing the shell and operculum. The bodies were then homogenized in approximately 0.1 ml of buffer (0.2 M Tris-HCl, pH 8.0). Water soluble enzymes were then absorbed on to  $6 \times 4$  mm rectangles of filter paper (Whatman No. 1), which were then placed in a slot cut across the gel. Constant voltages were supplied by Heathkit regulated H.V. power supplies (models 1P-17 and SP-17A). Running voltages were about 200V except for use with the Poulik (1957) buffer scheme which was run at a constant current of 40 mA. This was done to allow for the initial low resistance of the gel which would result in a relatively large current and undesirable heating effects. With the Poulik buffer system the resistance increases during running, thus permitting an increase in the applied voltage. The constant current was obtained from a 'Vokam' constant current, constant voltage D.C. power supply (Shandon SAE 2761). Gels were kept at *c.*  $2^{\circ}\text{C}$  during running. Running times were 4–5 h.

Staining methods were based upon those of Shaw and Prasad (1970) and Harris and Hopkinson (1978) but stain concentrations were somewhat increased. The aminopeptidase (*Ap*) stain used the dipeptide substrate *N*-glycyl-L-leucine. Malate dehydrogenase (*Mdh*) stain contained both nicotinamide adenine dinucleotide (NAD) and nicotinamide adenine dinucleotide phosphate (NADP) (NADP-dependent *Mdh* is also known as malic enzyme (*Me*)). Esterases were stained using a fluorescent staining technique (Harris and Hopkinson 1978). Loci staining by this method are called *Esterase D* by analogy to the fluorescent stained *Est D* locus in humans.

## RESULTS

**Morphological studies:** Measurements of the *L. aestuarii* specimens collected at Shottisham Creek are given in Table 1 and comparable data for the local populations of *L. obtusata* and *L. mariae* in Table 2. The *L. aestuarii* specimens ranged up to 9.6 mm in width, compared to 13.0 mm for *L. obtusata* and 8.4 mm for *L. mariae*.



The most striking feature of these *L. aestuarii* shells was the elevated spire in contrast to the almost flattened spires of *L. obtusata* and *L. mariaae*. This was measured as the spire angle (see Tables 1 and 2). The shell mouth was comparatively small and contracted, as shown by the shell aperture ratio, compared to the condition in *L. obtusata* and *L. mariaae*. The shell colour of the *L. aestuarii* specimens varied from fawn through brownish olive to dark olive. All these shells were thinner and more readily broken than is usual for either *L. obtusata* or *L. mariaae* shells.

When the specimens were dissected prior to electrophoresis it was revealed that three were male. The shape of the penis of one of these is shown in Fig. 2. It has a rounded tip and lacks a flagellum; the penial glands are arranged in one and a half rows and are rather bulbous. The penes of the other two males were similar. The number of penial glands on the three specimens was respectively 13, 14 and 16; representing a mean of 14.33 – lower than the mean for *L. obtusata* at any locality studied by Goodwin and Fish (1977), but higher than any for *L. mariaae*. The two females laid egg masses at 10 and 14 days respectively after collection.

*Enzyme Studies:* The specimens of *Littorina* used were successfully typed for a total of 17 enzyme loci, all coded for functionally different enzymes except for two *Ap* loci and three *Est D* loci. For convenience *Mdh* and *Me* were stained together. This combined stain showed the products of two loci, which were probably both *Mdh* loci; (Morris (1979) has shown two *Mdh* loci in *Littorina* spp.).

Three loci, *Acp* (acid phosphatase) *Got-2* and *Pgm-1*, gave inadequate enzyme activity to be scored unambiguously in all the samples (buffer systems used for these loci were 3, 1 and 1, respectively). The results obtained from the enzyme studies are summarized in Table 3.

At only one locus (*Pgm-2*) was there any observed difference in allele frequencies between *L. aestuarii* and *L. obtusata* (Table 3.). These differences were slight and well within the range of variation to be expected, on small sample sizes, from sampling error alone. Between these two populations and *L. mariaae* there were far greater genetic differences. Eight loci (*Mdh/Me-1*, *Mdh/Me-2*, *Idh*, 6 *Pgdh*, *Got-1*, *To*, *Ldh*, *Cat*) showed no differences and there were only slight differences in the allele frequencies of *L. mariaae* at the *Pgi* locus. However at five loci (*Mpi*, *Ap-2*, *Lap*, *Est D-1*, *Est D-3*) *L. mariaae* appeared to be fixed for different alleles and there were also substantial allele frequency differences for *Pgm-2*. The *Ap-1* locus of *L. obtusata* and *L. aestuarii* was apparently absent in *L. mariaae*, whilst the *Est D-2* locus of *L. mariaae* was apparently absent from the other two 'species'.

TABLE 1

*Littorina aestuarii* specimens collected near Shottisham Creek and examined by electrophoresis.

specimen no.	1	2	3	4	5
size group <sup>1</sup>	6	6	8	10	10
height (h)	6.9	7.0	9.0	10.2	13.4
width (w)	6.1	7.0	7.8	9.0	9.6
aperture (m)	5.2	5.25	7.0	7.4	7.3
spire (s)	1.7	1.75	2.0	2.8	6.1
spire angle (°)	107	102	105	100	75
shell aperture ratio (h/m)	1.33	1.33	1.29	1.38	1.84
lip	thin	thick	thin	thick	v. thick
weight (whole wet, g)	0.14	0.16	0.28	0.50	0.46
shell colour	fawn/olive	fawn	dark olive	fawn/olive	fawn/olive
body pigmentation	average	light	average	dark	light
sex	male	male	male	female	female

<sup>1</sup>Size group measured by passing through gauge with millimetre increment circular holes, other dimensions in millimetres.



TABLE 2

Timed (15 minute) collections of *Littorina obtusata* from near Bawdsey Manor, and *L. mariae* from Stonner Point, on the banks of the River Deben, Suffolk.

*Littorina obtusata*

Size group	4	5	6	7	8	9	10	11	12
no. of specimens	2	4	10	9	11	15	8	7	7
height (h)	3.6	4.8	5.8	7.0	7.9	9.1	10.5	11.8	12.6
width (w)	4.0	5.2	6.2	7.2	8.3	9.2	10.5	12.0	13.0
aperture (m)	3.4	4.4	5.2	6.2	7.1	8.1	8.7	9.2	9.0
spire (s)	0.2	0.4	0.6	0.8	0.8	1.0	1.8	2.6	3.6
spire angle (°)	165	148	153	141	149	150	142	140	139
shell aperture ratio (h/m)	1.05	1.09	1.11	1.12	1.11	1.12	1.20	1.28	1.40
lip	thin	thin	thin	thin	thin	thin	thin	thick	thick

*Littorina mariae*

size group	5	6	7	8
no. of specimens	3	26	16	1
height (h)	4.9	5.8	7.0	7.8
width (w)	5.1	6.0	7.0	8.4
aperture (m)	4.3	5.0	5.9	6.4
spire (s)	0.6	0.8	1.1	1.4
spire angle (°)	155	152	149	150
shell aperture ratio (h/m)	1.13	1.16	1.18	1.21
lip	thin	thin	thin	thick

The figures are means for each size group; definitions as in Table 1.

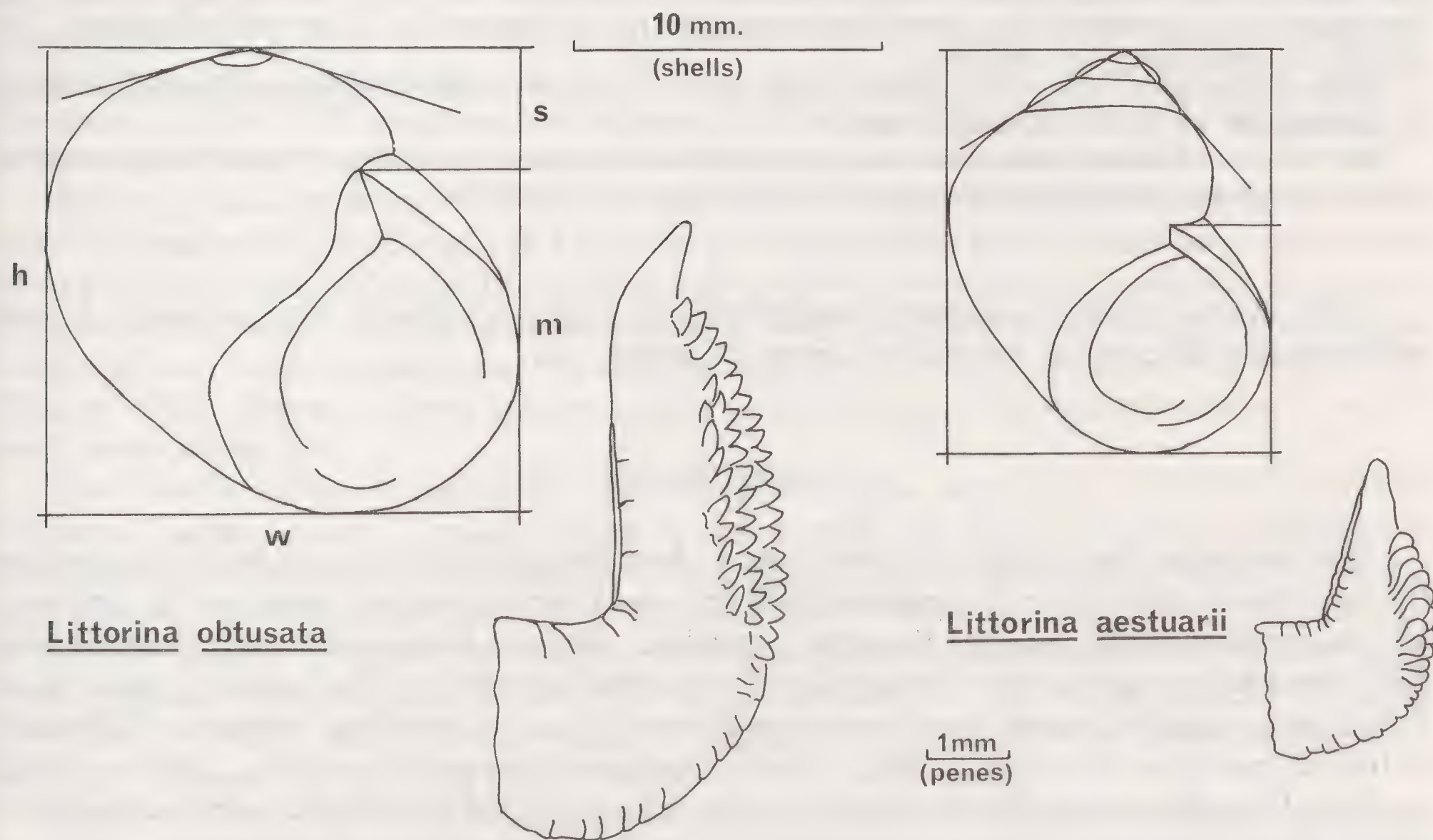


Fig. 2. Shell and penis features of typical specimens; h, shell height; w, shell width; m, shell aperture; s, shell spire height. Note method of measuring shell spire angle.



TABLE 3

Details of estimated allele frequencies and of buffer systems used for 17 enzyme loci in three 'species' of *Littorina*.

Enzyme Locus	Buffer System	Allele	Species		
			<i>obtusata</i>	<i>aestuarii</i>	<i>mariae</i>
<i>Mdh/Me-1</i>	2	1	1.00	1.00	1.00
<i>Mdh/Me-2</i>	2	1	1.00	1.00	1.00
<i>Idh</i>	2	1	1.00	1.00	1.00
<i>6 Pgdh</i>	3	1	1.00	1.00	1.00
<i>Pgi</i>	2	1	1.00	1.00	0.92
		2	0.00	0.00	0.08
<i>Mpi</i>	3	1	0.00	0.00	1.00
		2	1.00	1.00	0.00
<i>Got-1</i>	3	1	1.00	1.00	1.00
<i>Ap-1</i>	2	1	1.00	1.00	×
<i>Ap-2</i>	2	1	0.00	0.00	1.00
		2	1.00	1.00	0.00
<i>Lap</i>	3	1	1.00	1.00	0.00
		2	0.00	0.00	1.00
<i>Pgm-2</i>	1	1	0.92	0.70	0.00
		2	0.08	0.30	1.00
<i>Est D-1</i>	3	1	1.00	1.00	0.00
		2	0.00	0.00	1.00
<i>Est D-2</i>	3	1	×	×	1.00
<i>Est D-3</i>	3	1	1.00	1.00	0.00
		2	0.00	0.00	1.00
<i>To</i>	1	1	1.00	1.00	1.00
<i>Ldh</i>	1	1	1.00	1.00	1.00
<i>Cat</i>	1	1	1.00	1.00	1.00
<i>n</i>			12	10	12

Abbreviations used for loci, *Mdh* (malate dehydrogenase); *Me* (malic enzyme); *Idh* (isocitrate dehydrogenase); *6 Pgdh* (6-phosphogluconate dehydrogenase); *Pgi* (phosphoglucose isomerase); *Mpi* (mannose phosphate isomerase); *Got* (glutamate oxaloacetate transaminase; = *Aat* aspartate amino transferase); *Ap* (aminopeptidase); *Lap* (leucine aminopeptidase); *Pgm* (phosphoglucomutase); *Est D* (Esterase-D); *To* (tetrazolium oxidase); *Ldh* (lactate dehydrogenase); *Cat* (catalase).

Buffer systems are: 1 – tris-citrate, pH 8.3 (Poulik 1957); 2 – tris-citrate, pH 8.0 (Ward and Beardmore 1977); 3 – histidine, pH 7.0 (Fildes and Harris 1966).

Both loci and alleles are numbered in ascending order of electrophoretic mobility. *n* = sample size (number of alleles). × indicates the apparent absence of an enzyme locus in a population.

Thus overall whilst *L. aestuarii* was genetically indistinguishable for *L. obtusata*, it was substantially different at several loci from *L. mariae*.

## DISCUSSION

The first point that needs to be considered when discussing the present results is whether the specimens collected in September 1978 represent the population described by Jeffreys. His description reads; 'smaller than the typical (*L. obtusata*) form, uniform greenish-brown (the colour being more or less obscured by the excoriation or decay of the surface); spire more raised and compact; mouth more contracted, outer lip not expanding; sculpture slight and indistinct except in the young. L. 0.4 [inches]. Abundant between tide marks.' (Jeffreys 1869, p. 205). This description fits the specimens we collected (except that they were uncommon rather than abundant) and we feel justified in referring to them as *L. aestuarii*.

The habit of feeding on fucoids and laying gelatinous egg masses on these weeds indicates an affinity between *L. aestuarii* and the *obtusata/mariae* group rather than any other species



group of this large genus. It remains to examine whether there is sufficient distinction to warrant separate specific status.

The shell colour of *L. aestuarii* is unlike that normally seen in *L. mariae*. Although olivacea specimens of that species are said to occur, they are rare at best, and none was seen by Goodwin and Fish (1977) in their study of Norwegian and British Isles populations. *L. aestuarii* does not possess the long and distinctive terminal flagellum to the penis, the presence of which was the key feature in the separating *L. mariae* from *L. obtusata* by Sacchi and Rastelli (1966). So on morphological grounds *L. aestuarii* appears distinct from *L. mariae*.

The separation from *L. obtusata* is not so clear. The shell differences by which Jeffreys (1869) separated *L. aestuarii* from *L. obtusata* have been observed in this study but shell characteristics of *L. obtusata* vary, for instance with wave exposure (Goodwin and Fish 1977). In *Nucella lapillus* high spired forms are associated with very sheltered shores (Crothers 1977) and Shottisham Creek is extremely sheltered. Soft part differences of *L. aestuarii* include penial gland numbers (closer to *L. mariae*) and shape. But the numbers of penial glands are only just outside those quoted for *L. obtusata* (Goodwin and Fish 1977), and within those suggested for this species by Reimchen (1974).

By modern standards the morphological features examined are insufficient to resolve the taxonomic relationship between *L. aestuarii* and *L. obtusata*. Evidence from crossbreeding or ecological transplanting experiments would be time consuming to obtain and likely to be more questionable than enzyme electrophoresis.

The results of the enzyme studies show clearly that *L. aestuarii* is not genetically distinguishable from *L. obtusata* at any of the substantial number of enzyme loci which have been examined. However both *L. aestuarii* and *L. obtusata* differed considerably, over the same sample of loci, from specimens of *L. mariae*.

Genetic differences between species or populations may be quantified by any of several published methods to give a single figure indicating an overall level of similarity or dissimilarity. Table 3 shows the overall genetic differences at the enzyme loci used between the three 'species' of *Littorina*. These are quantified to give two measures of resemblance, genetic identity, *I*, (Nei 1972) and genetic similarity, *S*, (Thorpe 1979) (these are both on scales from 0 to 1 and are closely correlated) and two measures of dissimilarity, genetic distance, *D*, (Nei 1972) and genetic distance, *D*, (Thorpe 1979) (these are on scales of 0 to infinity and 0 to 1 respectively and are less closely correlated) see Table 4.

Investigations by many workers of enzyme differences between related species and between conspecific populations in a wide range of animal and plant species have shown that even between closely related sibling species the genetic differences are normally far greater than between conspecific allopatric populations. Different populations of a single species give values of *I* or *S* rarely much below 0.90 and typically about or above 0.95 (see Avise *et al.* 1975, Thorpe 1979). Between closely related species values of *I* and *S* are typically about 0.5 or 0.6 and rarely above 0.8.

Our results show an extremely high level of genetic similarity ( $I=0.997$ ,  $S=0.986$ ) between *L. obtusata* and *L. aestuarii* which is well outside the range of values expected from comparisons between even very closely related species. Such high values effectively indicate that the two populations are genetically identical and on these grounds alone *L. obtusata* and *L. aestuarii* must be considered conspecific. This conclusion is reinforced by the relatively high level of genetic differentiation between *L. obtusata/aestuarii* and the sibling species *L. mariae* ( $I=0.616$ ,  $S=0.607$ ), which can be readily distinguished genetically with the level of genetic variation between them being clearly within the expected range.

Observed values of *I* or *S* are subject to sampling errors. These are not easily calculated but are effectively a function of the number of enzyme loci sampled and on any practicable sample of loci are likely to be substantial (Nei and Roychoudhury 1974, Li and Nei 1975, Thorpe 1979). However on the value of *S* (0.986) obtained between *L. obtusata* and *L. aestuarii*



TABLE 4

Values of genetic identity ( $I$ ) and genetic distance ( $D$ ) (Nei, 1972) and genetic similarity ( $S$ ) and genetic distance ( $D$ ) (Thorpe, 1979).

	<i>L. obtusata</i> / <i>L. aestuarii</i>	<i>L. obtusata</i> / <i>L. mariae</i>	<i>L. aestuarii</i> / <i>L. mariae</i>	<i>L. obtusata</i> + <i>L. aestuarii</i> / <i>L. mariae</i>
$I$ (Nei, 1972)	0.997	0.606	0.623	0.616
$D$ (Nei, 1972)	0.003	0.501	0.473	0.484
$S$ (Thorpe, 1979)	0.986	0.600	0.615	0.607
$D$ (Thorpe, 1979)	0.014	0.400	0.385	0.393

the lower 68% confidence limit (equal in probability to  $S$  minus one standard deviation if  $S$  was a normally distributed variable) gives a value of 0.917. Therefore even allowing for sampling errors the value of  $S$  is still well outside the expected range of values between congeneric species and well within that found between different populations of a single species (Thorpe 1979).

Thus the finding of the electrophoretic studies of enzyme loci amplifies the impressions gained from morphological studies. *L. aestuarii* and *L. mariae* are distinct at the species level and *L. aestuarii* and *L. obtusata* are different morphotypes of the same species. From considerations of priority the name *L. aestuarii* must be regarded as a junior synonym of *L. obtusata*.

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# VARIATION WITHIN AND BETWEEN POPULATIONS OF *LITTORINA NIGROLINEATA* GRAY ON HOLY ISLAND, ANGLESEY

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**Abstract:** Populations of the rough winkle, *Littorina nigrolineata*, from a range of sites mostly on Holy Island, Anglesey, have been examined with respect to shell colour, shell shape, shell aperture width, penial gland number and shell size and thickness. In addition, reproductive investment has been investigated in four of these populations.

There is a remarkably disjunct distribution of the lined and unlined forms on Holy Island and on nearby Anglesey itself. At the one site at which both forms occur, the distinction between them is much less marked. There is a strong association between the broadness and squatness of shells and the exposure of the site at which they are found, and also between aperture width and exposure. Shell size and thickness both tend to be greatest at those sites with the greatest risk of shell injury by crushing. There is a surprising amount of variation in the number of penial glands. At a single site, Abraham's Bosom, two distinct populations (one occurring in crevices, the other amongst boulders) differ in their shell shape, shell size, shell thickness, aperture width, their size at maturity and their relative reproductive investment.

In all cases, these results are discussed in the context of the environmental selective forces acting on the winkles.

## INTRODUCTION

Of the four classically-defined species of British littorinids, *Littorina saxatilis* (Olivi) has the most variable shell and was described as one species with six subspecies and innumerable varieties until as recently as 1971 (for instance, by Berry 1961, James 1968, Pettit 1971). Two of these forms, *L. neglecta* Bean and *L. nigrolineata* Gray, were sufficiently distinct to be raised to species rank on the basis of reproductive characters, esterase patterns and shell type (Heller 1975a, Sacchi 1975), but attempts to define the rest of the *saxatilis* complex failed initially due to over-emphasis on shell characters. It is only very recently that the complex has been satisfactorily defined according to reproductive characters, ecology, distribution and to a lesser extent, shell characters, as four distinct sympatric species: *L. neglecta*, *L. nigrolineata*, *L. rudis* (Maton) and *L. arcana* Hannaford Ellis (Hannaford Ellis 1979).

*Littorina nigrolineata* is an autochthonous Atlantic boreal species, present all round Britain where the shore is suitable. The species occurs in the barnacle belt on exposed shores or associated with furoid algae on shores classed as sheltered by Lewis (1964), and attaches its egg masses to rocky substrates.

The shell is quite distinct, having a broad, flat-ridged pattern separated by narrow grooves. The shell colour is commonly yellow, though often white; and, more rarely, populations of reddish-shelled animals occur, usually cryptically associated with red sandstone (Heller 1975b). These three ground colours are readily distinguishable as separate morphs. The shell may be either plain coloured (var. *compressa* Jeffreys) or with the grooves pigmented brown or purple, producing a characteristic lined or striped appearance, hence *nigrolineata*. The species is interesting in that, on most shores where it is found, each

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population comprises either all var. *compressa* or all var. *nigrolineata*; few mixed populations occur.

The aims of this study were threefold:

1. To map the distribution of the varieties *compressa* and *nigrolineata* on Holy Island, Anglesey; to discover any points of transition, whether disjunct or maintained as a cline; and to survey any mixed populations found, noting their varietal proportions and their relation to pure populations.
2. Bearing in mind the oviparous habit of *L. nigrolineata*, and thus its very limited powers of dispersal and its potential for producing localized adaptations to the environment, to assess the extent of intraspecific variability and the morphological variation between geographically separated populations.
3. To examine as far as practicable the biotic and abiotic factors affecting microgeographically localized populations, and the extent of adaptive divergence within one exposed shore on Holy Island.

## MATERIALS AND METHODS

*Localities.* Holy Island, Anglesey was chosen as the main study area, as it is small enough for a survey of its 45 km coastline, yet large enough to experience a wide range of exposure to wave action. The study thus covered biotopes ranging from extremely sheltered sandy shores with isolated rock outcrops, to extremely exposed rock and boulder shores with differences in gradients producing accentuation of tidal effects.

Holy Island lies off the west coast of Anglesey and is approximately 9.5 km in length. Its width varies from just 1 km at its waist to a maximum of 7 km south of Holyhead. The island itself is relatively flat apart from the north-west corner of the island, where there is a stretch of 4 km of sheer cliffs 30–110 m in height with virtually no access to the shore line either from the land or along the coast (Fig. 1). Except for the east coast, adjacent to Anglesey, where the sheltered sand and mud flats produce a habitat that will not support littorinids, the coast of the island is heterogeneous, consisting of many small sandy or rocky bays isolated from one another by stretches of cliffs which can only be reached directly from the sea.

*Sampling.* Twelve shores on which the presence of *L. nigrolineata* has been established (Fig. 1) were randomly searched, and the percentages of the varieties *compressa* and *nigrolineata* were scored. At four sites, selected because of differences in topography, exposure, and varieties present, random samples of 60–100 specimens were collected from an area as small as possible; and at one of these sites – Abraham's Bosom – samples were taken on one day from two disjunct *L. nigrolineata* habitats 30 m apart up the shore: one was amongst fairly large boulders, the other was in the crevices of a rocky stack. The sampling areas were chosen in relation to topography and the abundance of specimens. Notes were taken of shore topography, gradient, and the height on the shore of the sample with regard to mean high water (MHW). The exposure of each shore sampled was determined by considering physical and biological characters according to Ballantine's scale for rocky shores from 1 (extremely exposed) to 8 (extremely sheltered). All samples were taken alive to the laboratory.

Further samples were obtained from two sites on Anglesey itself: Porth Penrhyn Mawr, 1 km across the bay from the north end of Holy Island, and Porth Llanlana on Anglesey's north coast. A sample was also received from Scotland, collected from a harbour wall at Dunbar. There was, therefore, a total of eight samples which were examined in detail.

Details of all sampling stations are given in the Appendix and, where appropriate, with the tabulated results.

On return to the laboratory, specimens were boiled for 30 seconds before examination. In





SAMPLED

100% LINED  
VAR. NIGROLINEATA

100% UNLINED  
VAR. COMPRESSA

MIXED POPULATION

SURVEYED



SAND AND MUDFLATS

Fig. 1. Location of sites on Holy Island and nearby Anglesey; and the distribution of the lined and unlined forms of *Littorina nigrolineata*.



order to preserve specimens, the columellar muscle was broken after boiling and the material was stored in 70% alcohol.

*Characters measured.* Measurements of various aspects of the shells' shape were taken with dial vernier calipers accurate to 0.05 mm, and then rounded off to the nearest 0.1 mm. The following measurements were taken (Fig. 2): maximum shell height (SH), shell diameter (SD), aperture height and diameter (AH, AD). The first two dimensions were used to calculate the Spire Index  $SH/SD$  as a measure of shell shape (Cain 1977). Aperture width, standardized to take account of shell size, was calculated from  $AD/AH$  (since Heller (1975a) and James (1968) both found that AH is proportional to SH—a result confirmed in the present data).

The shell was oven-dried to constant weight, and dry weight determined to the nearest 0.001 g. For each sample, the percentage of shells that had been previously damaged by crushing or predator attack and survived to continue growth (Fig. 1 of Raffaelli 1978) was determined, and the percentage of white morphs was also determined. Using a binocular microscope at constant magnification and a graduated eyepiece, penis length and number of penial glands were determined for males (Fig. 3), and the dimensions of the females' pallial oviduct measured in order to estimate reproductive capacity or investment (see below) (Fig. 4). The measurements were recorded in their arbitrary units for comparative purposes and not converted from the calibration of 10 mm=6.1 units. For individuals from the two Abraham's Bosom samples, and those from the Dunbar and Penrhyn Mawr samples, the whole body was oven-dried to constant weight to the nearest 0.001 g.

*Shell thickness.* Thickness of shell was not measured directly, but an analogue of it may be calculated from measurements of other factors to which it is related, since it is possible to consider shell thickness,  $T$ , as a function of other shell dimensions and shell dry weight (wd). Specifically, shell weight can be thought of as compounded from shell thickness and the volume defined by the outside of a shell,

i.e.  $wd = T \times SH \times \text{shell width} \times \text{shell breadth}$ ,  
or, approximately,  $wd = T \times SH \times SD^2$ .

$T$  has been computed in this way for each individual, and the mean shell thickness estimated for each site.

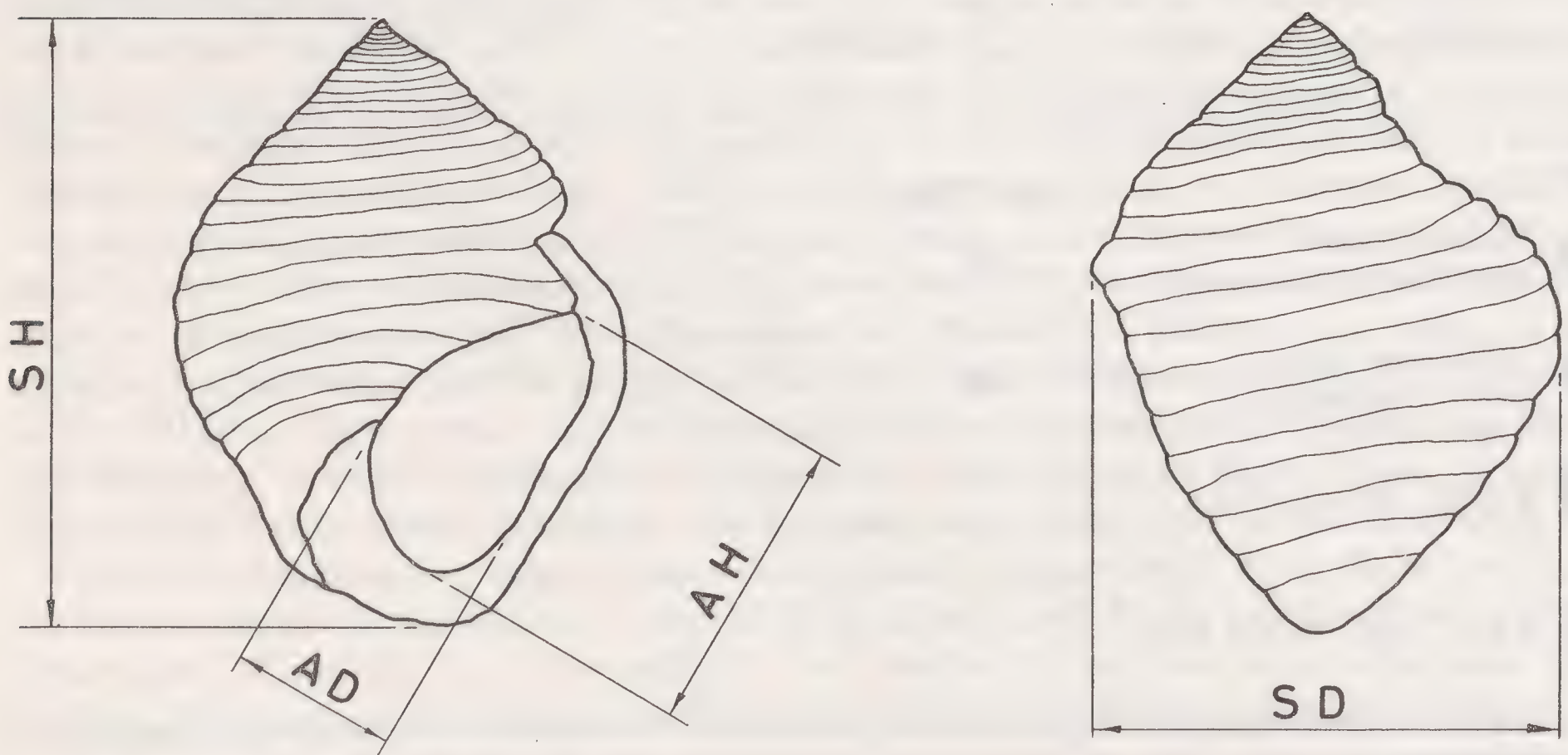


Fig. 2. Shell dimensions used in this paper. SH: shell height; SD: shell diameter; AH: aperture height; AD: aperture diameter.



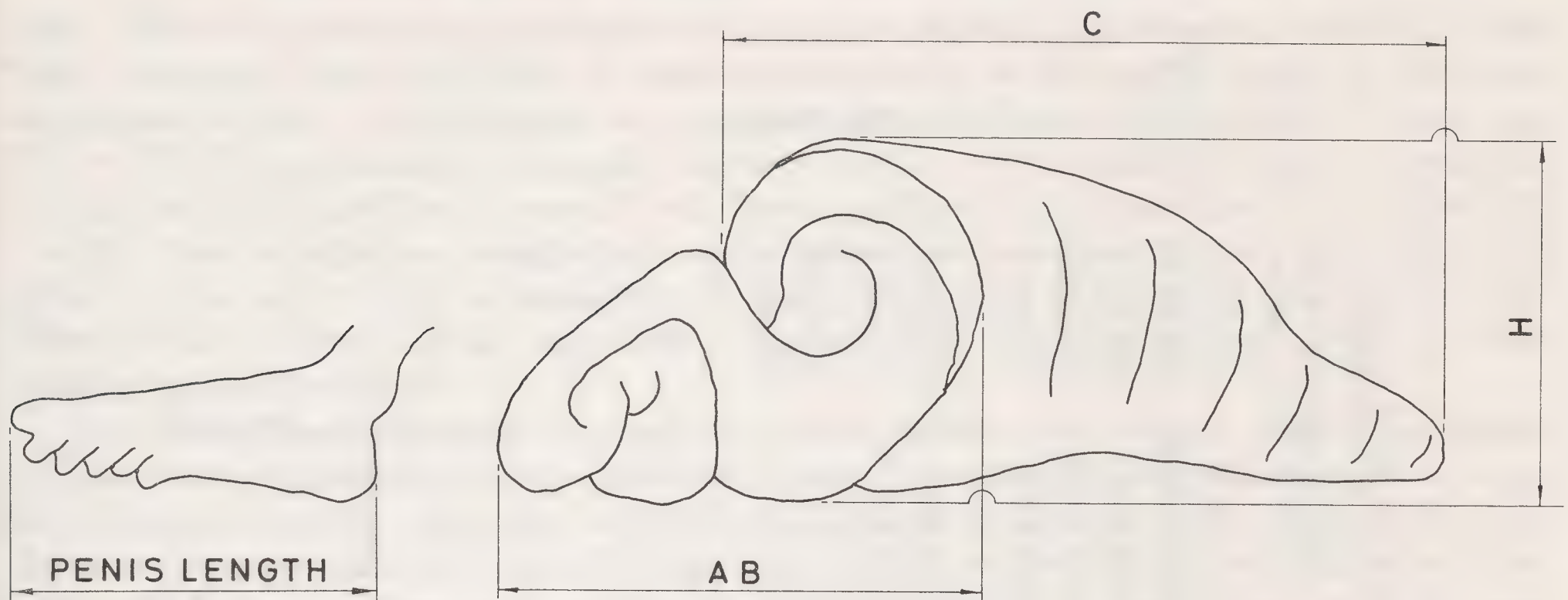


Fig. 3. 'Penis length' of *L. nigrolineata* used in this paper.

Fig. 4. Diagrammatic representation of the pallial oviduct of *L. nigrolineata*. AB: length of albumen gland (left) and capsule gland (right); C: length of jelly gland; H: maximum height.

*Reproductive capacity.* Because *L. nigrolineata* is oviparous, it is not possible to measure fecundity directly by examining the contents of a brood pouch. However, it is possible to estimate the proportion of total body weight devoted to the reproductive system (Fig. 4). The length of albumen and capsule glands (AB), and the jelly gland (C) can be summed, and then multiplied by the mean height of the whole pallial oviduct (H) to give an estimate of sagittal section area. This raised to the power  $3/2$  produces an estimate of volume. If this is divided by dry body weight, an arbitrary comparative measure of reproductive investment (R) is obtained,

$$\text{i.e. } R = \{(AB + C)H\}^{3/2} / \text{dry body weight}$$

This determination of reproductive investment was applied to two crevice-inhabiting populations – Dunbar (var. *compressa*) and Abraham's Bosom (var. *nigrolineata*) – and two free-living boulder populations: Penrhyn Mawr (var. *compressa*) and Abraham's Bosom (var. *nigrolineata*). All samples were collected within five days of one another in January/February 1978, reducing any confounding effects of seasonal variation.

## RESULTS

### *Distribution of varieties compressa and nigrolineata.*

*Littorina nigrolineata* has a remarkably disjunct distribution of the varieties *compressa* (unlined) and *nigrolineata* (lined) on Holy Island (Fig. 1, Table 1), and indeed, of all the sites surveyed, only one had a population consisting of both varieties occurring sympatrically: that at Porth Llanllana on the North Anglesey coast where *compressa* occurred as 69% of the sample and *nigrolineata* 31%.

This distribution, however, is far from haphazard. The area of 100% lined extends down the west coast of Holy Island, from the north side of South Stack round to the furthest point of littorinid occurrence at Silver Bay, beyond which the sand and mud flats exclude the species along the coast adjacent to Anglesey. The area of 100% *compressa* extends from the north-east side of North Stack across the northern coast of the island, and continues up the Anglesey



TABLE 1

Sample sites, their exposure, and details of the *L. nigrolineata* samples collected. (For further site details, see the Appendix.)

Population	Sample size	Exposure (Ballantine's scale)	percentage <i>nigrolineata</i>	percentage white	total sample			shells between 11.5 mm and 15.1 mm in height	
					mean shell thickness±SE	mean shell height±SE	mean shell thickness±SE	mean shell height±SE	percentage damaged
Abraham's Bosom (boulder)	84	1	100	4	3545±31	14.7±0.17	3546±40	13.8±0.13	37
Abraham's Bosom (crevice)	69	1	100	0	2852±72	9.9±0.25	3021±113	13.3±0.30	6
Ynys Wellt	98	3	0	3	3415±37	13.9±9.19	3390±42	13.5±0.11	20
Dunbar (crevice)	61	4	0	0	2991±31	9.6±0.17	—	—	11
Treaddur Bay	83	5	100	26	3965±33	15.6±0.18	3914±69	13.9±0.15	21
Penrhos	61	6	0	18	3554±33	14.1±0.35	3491±31	13.1±0.17	33
Porth Penrhyn Mawr	77	7	0	0	3777±28	16.8±0.30	3641±133	13.3±0.64	29
Llanlana	67	8	31	19	3175±31	12.4±0.13	3168±35	12.6±0.12	30

TABLE 2

Size of maturation at Abraham's Bosom.

	Boulder population		Crevice population	
	♂	♀	♂	♀
Minimum mature height (mm)	11.5	12.3	7.5	7.9
Maximum immature height (mm)	14.8	12.7	8.7	8.3
Average	13.2	12.5	8.1	8.1



coast. The survey leaves a gap between the two areas of only 3 km between South Stack and Porth Namarch unresolved due to sheer inaccessibility of the shore except to the most experienced climber. Nevertheless, the transition of North Stack is undoubtedly a rapid one. Heller (1975b) by obtaining a sample from the west side of North Stack, appears to suggest that the point of transition is around North Stack itself, a length of less than 1 km of sheer 100 m cliffs. Most populations sampled are isolated from one another by barriers of a physical nature—either sheer cliffs, or areas of sand and mud that do not support littorinid species. There is no evidence of an association between this distribution and those of other morphological characters.

The effect of the lined pigment on yellow or white shells is very striking, and the lined form occurs on both exposed and fairly sheltered shores (Treaddur Bay, for instance), but not on the sheltered extremes where the unlined form is found. At Treaddur, the lined shells were abundant in association with fucoid algae on rock outcrops, but on very exposed shores they were only found on open rock with well developed barnacle cover. One such site was Abraham's Bosom where the lined form was abundant on open boulders, and the pigment, compared with the Treaddur population, was particularly well developed. On such a shore, the yellow unlined forms might be particularly obvious; whereas the pigment may serve to break up the outline of the shell shape against a rock-and-barnacle background, and may possibly lead to a resemblance to the dark sutures between barnacle plates.

The mixed population of Llanlana occurred on a very sheltered shore, thickly covered with brown algae, and variety *compressa* predominated. The difference in the pigmentation of the nigrolineate forms present was striking compared to the purely lined populations at Treaddur and Abraham's Bosom. In all lined specimens at Llanlana the pigment was very much lighter in colour and discontinuous around the whorls of the shell. Moreover, there was a gradation of pigment between individual shells, ranging from light to almost invisible, that did not occur in pure populations. No strongly lined forms were found on a detailed survey of this shore. There was no indication that the proportions changed over the shore any more than would be expected from chance alone. In a few individuals, the purple-brown lined pigment had spread over the shell, grading into the background coloration, producing a broadening of the 'lines' into 'bands'.

#### *Variation between populations*

*Occurrence of white morphs.* White morphs were found in five out of eight populations sampled, but proportions greater than 15% were found at only three sites: Treaddur, Penrhos and Llanlana. The white shell is particularly striking, especially the lined form, and these substantial proportions were only found on shores with a thick rock cover of fucoid algae, i.e. sheltered shores. The lined form at Treaddur occurred at a high frequency of 26% on stable rock outcrops beneath the attached algae. Both lined and unlined white morphs occurred at Llanlana, also in close association with brown algae.

White morphs were not found on exposed shores devoid of algal cover, except at Ynys Wellt on the exposed rock face where a frequency of three in ninety eight was recorded. These individuals were very obvious against the background rock.

*Spire Index SH/SD.* As a measure of shell shape, the spire index indicates whether shells are relatively tall, or broad and squat. A good correlation of spire index with exposure and habitat is demonstrated by Fig. 5. On the most sheltered shores—Llanlana and Penrhos (exposure grades 8 and 6 respectively)—mean spire index reaches 1.22; but on exposed shores (exposure grades 1–3) this drops to 1.17 to 1.18. It is particularly interesting to note that where *L. nigrolineata* adopts a crevice habit at Dunbar (exposure, 4) and Abraham's Bosom (1), the spire index is further depressed, as a response to the selection forces this specialized habitat imposes (Fig. 5).



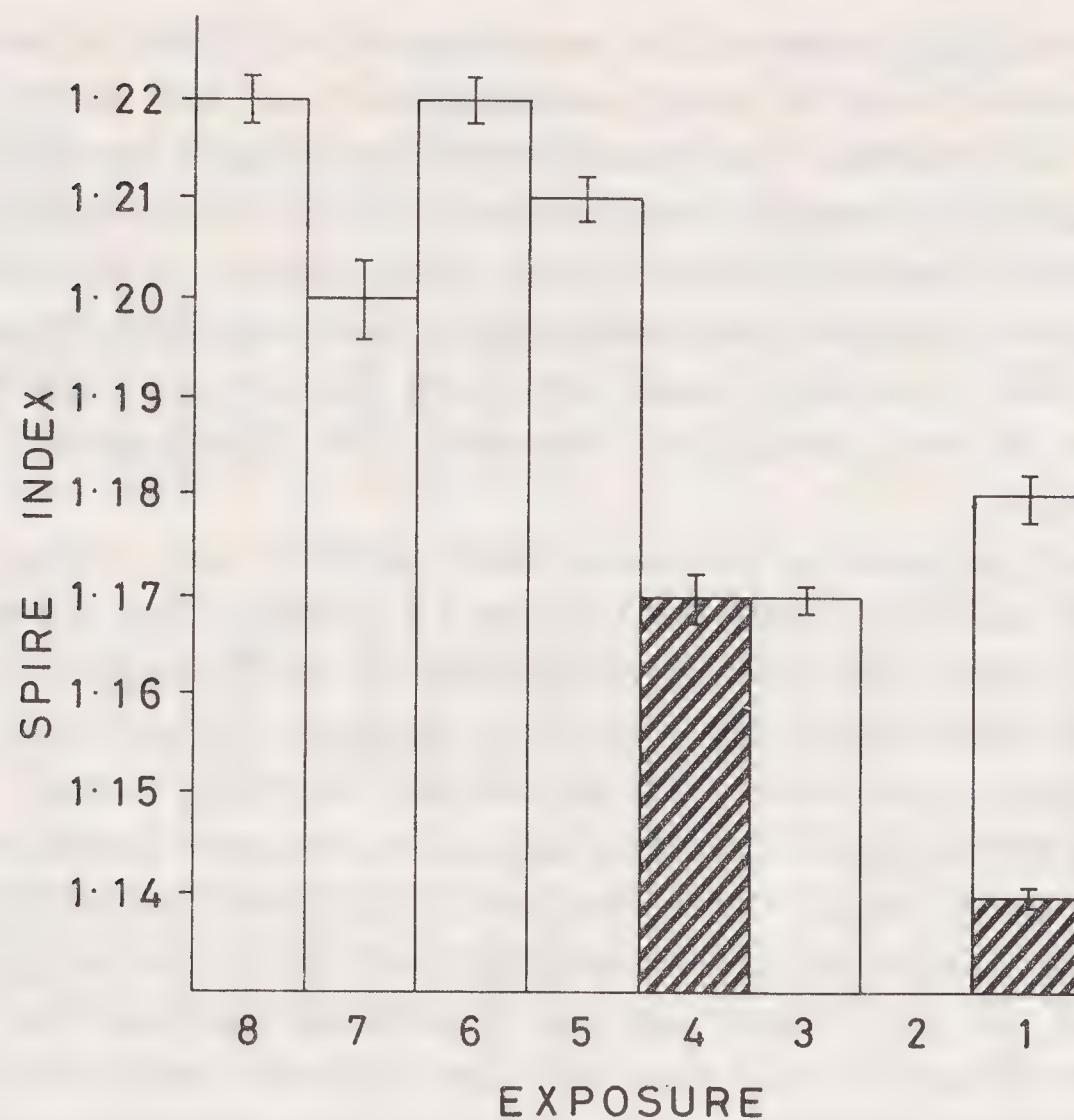


Fig. 5. Variation of mean spire index (standard errors attached) with exposure; unhatched: free-living populations; hatched: crevice populations.

A marked sexual dimorphism of shell shape is demonstrated in many populations, females being squatter and broader than males. t-tests indicate that these differences are significant at Ynys Wellt ( $p < 0.01$ ), Abraham's Bosom ( $p < 0.05$ ) and Penrhyn Mawr ( $p < 0.05$ ).

*Aperture width AD/AH.* Aperture width gives a measure of narrowness or roundness of the shell aperture for an animal of a given size, and thus measures the relative area of direct contact of the animal with its environment. A positive association of wider, rounder aperture occurs with increased exposure (Fig. 6). The association is also with another aspect of habitat, however, since on sheltered shores, with smaller aperture widths, there is more sand surrounding the sampled rock and pebble sites. (This is especially true at Penrhos and Penrhyn Mawr). Avoidance of sand as an irritant inside the shell of a marine gastropod may be an important factor in its ecology. On shores very exposed to wave action, where adhesion of the foot to the rock is important and sand is absent (Abraham's Bosom, Ynys Wellt), the aperture is wider and rounder. The adoption of a crevice habit at Abraham's Bosom has reduced exposure and the crevice population has a smaller, narrow aperture with a mean width of 0.77 compared to the largest figure of 0.81 for the boulder population.

The intraspecific variations in spire index and aperture width are small, but the attached standard errors indicate that the associations are real. This suggests that selective pressures have led to significant adaptation to the environmental extremes observed.

*Penial gland number.* As might be expected, there is no obvious overall correlation between either penis length or penial gland number, and habitat or exposure. However, Fig. 7 indicates a marked increase in this latter character on the sheltered shore at Penrhyn Mawr (exposure 7), and in the crevice population at Dunbar (exposure 4). This variation between populations may largely be a non-adaptive result of their historical isolation from one another, or may be a response to some unknown factor or combination of factors. However, since penis characteristics can be used to aid identification amongst the four sympatric species of rough winkle (Hannaford Ellis 1979), though not diagnostically, such variation is certainly noteworthy.



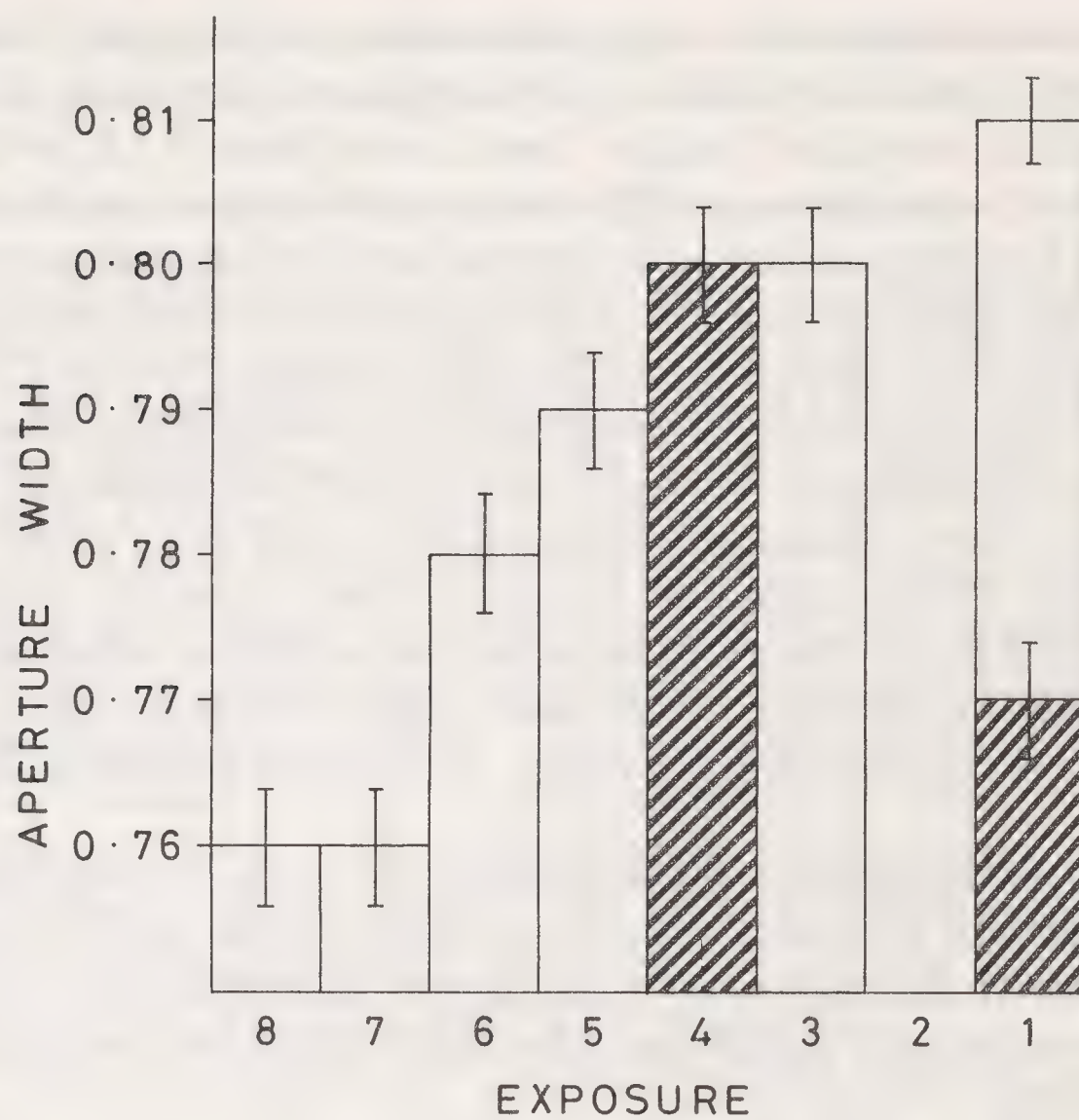


Fig. 6. Increase in aperture width (standard errors attached) with exposure; unhatched: free-living populations; hatched: crevice populations.

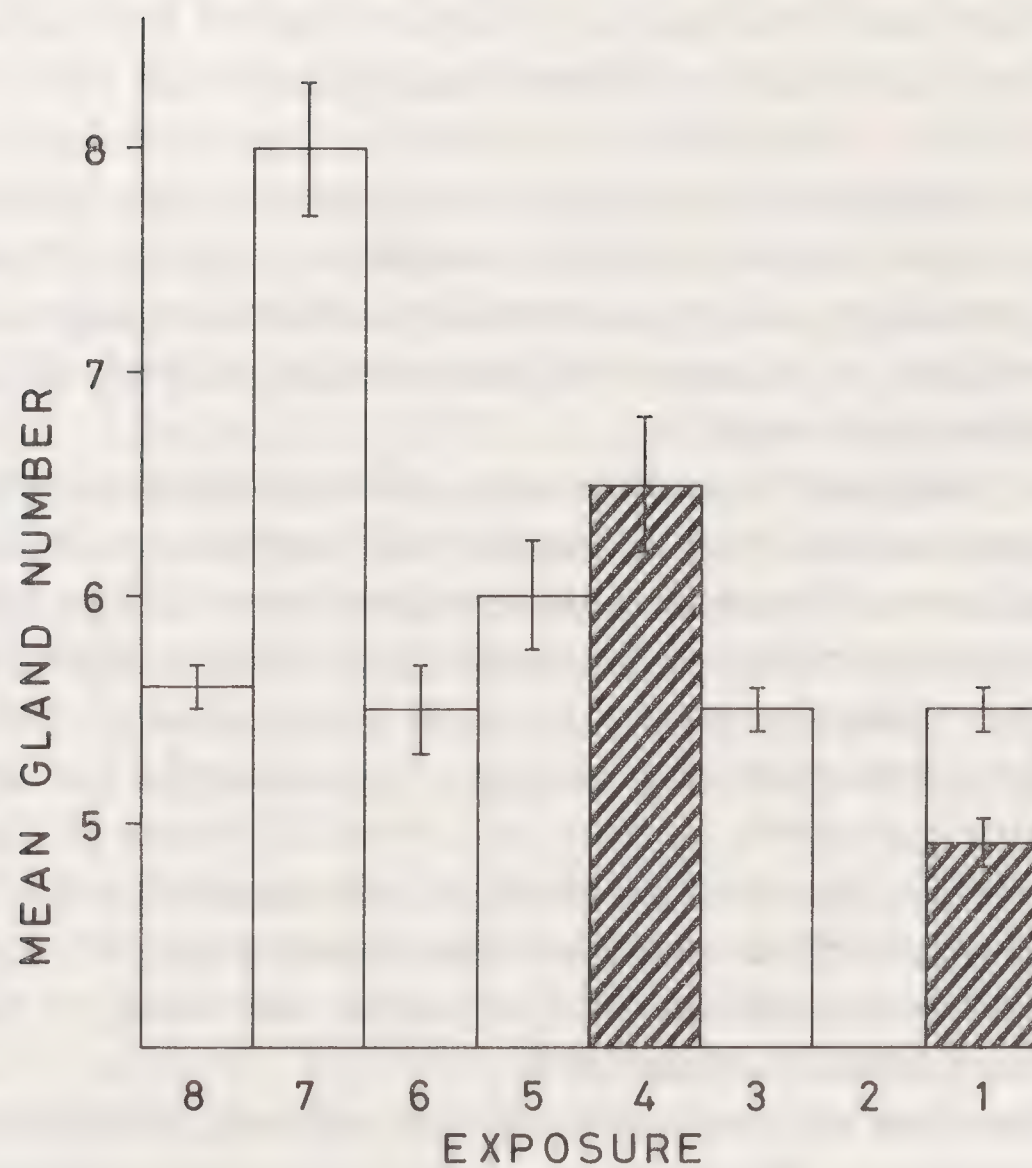


Fig. 7. Variation in mean penial gland number (standard errors attached) with exposure.



*Shell thickness.* Shell thickness has been computed on an arbitrary scale ( $w.d./SH. \times SD^2 \times 10^7$ ) and varies between 3965 and 2852 (Table 1). It is apparent, however, that thickness at a site is very highly correlated with shell height (rank correlation 0.93,  $p < 0.01$ ); and it is not immediately clear whether site-to-site differences in thickness are the result of this, or of additional localized adaptation affecting thickness itself. In an attempt to compare shells of similar height, therefore, shell thickness and shell height have been recomputed for each site, restricting the sample to those shells lying in the height range 11.5 mm–15.1 mm. These limits were chosen because they represent the heights of the smallest Abraham's Bosom boulder shell and the largest Abraham's Bosom crevice shell respectively; and because it is particularly important that meaningful samples are taken from these Abraham's Bosom populations (see below). This range has allowed revised estimates to be made from large samples (28 or more) for five of the eight populations, and from samples of 12 and 5 for the populations of Abraham's Bosom crevice and Porth Penrhyn Mawr respectively. The Dunbar individuals were too small for this range. The results are shown in columns 7 and 8 of Table 1.

The revision of the estimates has very little effect on the shell thickness values, and indeed the rank order is essentially unchanged (rank correlation 0.96,  $p < 0.01$ ). On the other hand, the revision has equalized the shell height values very markedly, and to such an extent that there is no longer a statistically significant association between height and thickness (rank correlation 0.60,  $p > 0.05$ ).

It seems, in other words, as if animals of comparable size (though admittedly unknown age) differ in shell thickness from site to site, and that Treaddur Bay > Porth Penrhyn Mawr > (Penrhos and Abraham's Bosom 'boulder') > Ynys Wellt > Llanlana > (Dunbar and Abraham's Bosom 'crevice').

Shell thickness appears to be correlated with both shore topography and shore exposure. The thinnest shells certainly occurred in crevice populations. The thicker shells are apparently associated with mobile substrata, high values on the biological exposure scale, and (conceivably) with exposure to the prevailing westerly wind. Thus, particularly thick shells occur on the west-facing shores at Treaddur and Penrhyn Mawr; the mobile pebble beaches at Penrhyn Mawr and Penrhos have thicker-shelled individuals than those on the more stable boulder shores at Abraham's Bosom and Llanlana; and amongst the sites with intermediate-thickness shells, the thickest occurred at the most exposed site (Abraham's Bosom, 'boulder') and the thinnest at the least exposed site (Llanlana). Increases in exposure and increases in the mobility of the stones on a shore are both likely to lead to increases in the risks of crushing – a known mortality factor in winkles (Raffaelli and Hughes 1978). There seems, therefore, to be an overall association of thick shells with high-risk sites and of thin shells with low-risk ones.

In addition, however, thick shells are known to afford protection against predation (Elner and Raffaelli 1980), and some of the site-to-site differences in thickness may be due to differences in the abundance and specific nature of predators. These were not studied; but it certainly appears likely that, by virtue of being relatively inaccessible, the crevice-inhabiting winkles are relatively free from the predation of at least some of their predators.

Shell damage (resulting from partial crushing or unsuccessful predatory attacks) that has been repaired by subsequent growth, appears as a marked suture in the vertical plane of the shell (Fig. 1 in Raffaelli 1978). However, while there are comparatively few damaged shells in the thin-shelled populations, there is no correlation between percentage damaged and either habitat differences or thickness differences amongst the sites of the intermediate and thick-shelled populations (Table 1, column 9).

Finally, Table 1 shows that the rank order of sites with regard to mean shell height is very similar to that for shell thickness. There is also, therefore, an overall association of large shells with sites at which the chances of crushing are high. Conclusions from these data must be



particularly tentative, however, because the smallest individuals at each site were not collected, and the size-range of these individuals differed from site to site.

*Variations within populations: localized adaptation at Abraham's Bosom*

Localized adaptation to habitat is particularly marked at Abraham's Bosom, where there is an unstable boulder habitat on the upper shore, and a creviced crag or stack only fully exposed at low water (see Appendix). Mean spire index is low overall on this exposed shore, but further significant depression occurs in the crevice population: 1.14 in the crevice population compared to 1.18 in the boulder habitat ( $p < 0.001$ ). Also, the mean aperture width in the crevice population decreases from 0.81 to 0.77. The necessity for maximum foot adhesion in response to an exposure grade of 1 is reduced in a crevice.

Shells from the boulder population are significantly thicker and significantly larger than those from the crevice population (Table 1). The boulder population experiences crushing and predation limited mainly by the crypsis afforded by the lined shell against the barnacle/rock background. These crushing and predation pressures are associated with a high proportion of damaged shells (37%). The crevice population, on the other hand, experiences no crushing and is relatively protected, by physical features, from predation. Only 6% of the shells in the crevice sample were damaged.

The calculation of  $R$  as an estimate of reproductive investment in these two populations leads to values ( $\pm$ S.E.) of  $797 \pm 37$  and  $685 \pm 36$  for the crevice and boulder populations respectively ( $d = 3.25$ ,  $p < 0.002$ ). Interestingly, the reproductive investment in the other 'crevice' population (Dunbar) was also high ( $729 \pm 29$ ); while that in the thick-shelled Porth Penrhyn Mawr population was very low ( $552 \pm 30$ ).

The mean size at which maturity was attained in each population was determined as the mid-point between the smallest mature and largest immature individual and the results are shown in Table 2. These clearly indicate that maturity amongst boulder individuals is achieved at a size beyond that which the crevice individuals show breeding to be possible.

## DISCUSSION

Heller (1975b), in a survey of the north-west coast of Anglesey for what were termed morphs of *L. nigrolineata*, found a similar situation to that described here. Two mixed populations with low frequencies of lined forms were distributed between shores of 100% unlined populations. The geographical nature of coastal topography in this area, however, was a less effective barrier than the sheer cliffs and mud flats on Holy Island, and migration of individuals between shores must have been more likely (though still rare). The oviparous habit of *L. nigrolineata* favours localized adaptation by severely limiting dispersal of the young from the parental habitat. However, the size of the panmictic unit of this species has not been determined and knowledge of this would greatly facilitate a study of the ecology of this animal. Anderson (1974) attempted to determine the panmictic unit size of *L. neglecta* (a much smaller species) on Anglesey and suggested a circle of approximately two metres diameter.

Usually the lined/unlined character has been defined as a polymorphism, but the strict definition of Ford (1940) is of the occurrence together in the same locality of two or more discontinuous forms of a species in such proportions that the rarest of them cannot be maintained by recurrent mutation. This does not occur at Llanllana where the two varieties occur sympatrically, and the patterns of pigmentation are less well defined and tend to break down, reducing in intensity and producing a series of grades of pigmentation to the unlined form. At Church Bay on the west coast of Anglesey (a site that has been regularly and



intensively sampled over a period of two years as a persistently 100% unlined population) two nigrolineate juveniles were found on one occasion recently (Hannaford Ellis, personal communication). These presumably appeared via a vector from a lined population or as rare mutants, and may be precursors of the situation currently found at Llanlana. On Holy Island, two major physical barriers act to isolate the areas of distribution of the lined and unlined forms. There is a very sharp transition from 100% lined to 100% unlined over a 1 km stretch of sheer-cliff coastline from North Stack to Porth Nanarch; while the southern extreme of the distribution of the lined form is isolated from the northern distribution of the unlined form by a stretch of sand and mud flats along the east coast of the island – a habitat that does not support littorinid species. This distribution may reflect the long-standing habitat isolation and the restriction on migration and gene flow. On the other hand, migratory and mutational events, though rare, are almost bound to have occurred in the past. The possibility that these disjunct distributions are maintained by selection, therefore, cannot be ignored. It seems certain that further study of distributions like the one described on Holy Island could be profitable.

It is reasonable to expect that many of the variations in shell height and shape found in this study afford some survival value, especially in environmental extremes. The selective advantage, for example, of low-spined, large-apertured shells on exposed shores experiencing severe wave action seems obvious once the environmental factor is identified; such shells are less likely to be dislodged. Similarly, variation in shell thickness is apparently related to the amount of crushing (and perhaps predation) which is likely to be experienced. Moreover, large shells are also comparatively resistant to crushing and predation (Elner and Raffaelli 1980). It is, therefore, to be expected that where the risk of injury is high, winkles will put a relatively large amount of energy into growth, and a smaller amount into reproduction, and will consequently be larger on average. (For further discussion, see Hart and Begon 1982).

Of the predators, the rock pipit, *Anthus spinoletta* Montagu, is the final host of the digenean parasite *Microphallus pygmaeus* Levinsen, whose larval stages are found in Britain only in *L. nigrolineata* and *L. rudis* (Heller 1975b), and it is particularly abundant on Holy Island around North Stack. It is likely to have good colour vision in parts of the spectrum, and Heller (1975b) has suggested that it may employ visual selection on *L. nigrolineata*, taking juveniles in large numbers. In addition, the shore crab, *Carcinus maenas* L. (the intertidal host of *Microphallus similis* Jägerskiöld whose larval stages are also found in *L. nigrolineata*) preys upon larger specimens of winkles.

The divergence in penial gland number discovered in isolated populations is potentially of great significance, though not correlated to an environmental factor. *L. nigrolineata* is commonly reported as possessing four to seven large penial glands on a characteristically developed penis, while the males of other, closely-related species have characteristically large numbers of small glands extending along the penis (Hannaford Ellis 1979). It was noticeable that penes of *L. nigrolineata* examined from Dunbar and Penrhyn Mawr, with twelve or thirteen glands, closely resembled those of *L. rudis* which occurred sympatrically. This, and the variation in penis anatomy between isolated populations, make it clear that gland number cannot be considered diagnostic in this case.

Localized adaptation to the environment is favoured in isolated shore populations which experience very different exposures to climatic extremes and predation. If the species is mobile and can reach all parts of its shore, then the formation of a distinct local race appropriate to each shore is possible; but in many winkles, with their very restrained mobility and dispersal, further localization of adaptation can occur. The selection forces operating in the crevice and boulder habitats at Abraham's Bosom have produced two specifically-adapted forms of the species. The crevice population has thin shells, low spires, small, narrow apertures, small body size, less delayed maturity and a significantly higher reproductive investment; while the boulder population has thick shells, tall spires, large, rounder



apertures, large body size, delayed maturity and a lower reproductive investment. This divergence is discussed by Hart and Begon (1982), but some comments are appropriate here. In the crevice population, with its relatively constant climate and relative freedom from predation, competition for space must be intense (see Hart and Begon 1982). This competition is largely absent in the boulder populations, and climatic variability and predation are the major limiting factors. Life-history strategy theory (see Stearns 1977) might lead us to expect reproductive strategy to be appropriately adapted to each environment, i.e. large numbers of small offspring in boulder populations; and lower numbers of larger offspring in crevice populations. However, it is difficult to ascertain in this oviparous species whether the increased reproductive investment in crevice populations is directed to increased egg size, or to a simple increase in egg number. A study of egg masses identified as *L. nigrolineata* is necessary to determine reproductive strategy.

#### ACKNOWLEDGEMENTS

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#### APPENDIX

*Details of sampling stations and dates of collection.*

1. *Abraham's Bosom*, Holy Island. Grid Ref. SH215814. 3.2.78. Boulder/rubble shore facing south-west, slight gradient. Exposure scale 1. Samples collected amongst boulders 10 metres below MHW.
2. *Abraham's Bosom*, Holy Island. Grid Ref. SH215814. 3.2.78. A creviced crag, facing south-east. 30 metres down shore from above sample. Samples collected from three crevices at similar heights on crag, 2 m apart.
3. *Ynys Wellt*, Holy Island. Grid Ref. SH233839. 12.10.77. A stable rock face facing south-west. Exposure scale 3. Samples collected along a transect between MHW and MLW.
4. *Dunbar*, Scotland. Grid Ref. NT680795. 27.1.78. A harbour wall, facing north-east. Exposure scale 4. Samples collected from crevices on splash zone.
5. *Treaddur Bay*, Holy Island. Grid Ref. SH255786. 22.11.77. A sandy beach facing west. Exposure scale 5. Samples collected from isolated rock outcrops at south end of beach.
6. *Penrhos*, Holy Island. Grid Ref. SH266817. 22.11.77. A sandy beach facing north-east. Exposure scale 6. Samples collected from the east end of the beach at a small boulder and pebble site isolated by sand from the rest of the beach.
7. *Penrhyn Mawr*, Anglesey. Grid Ref. SH285838. 3.2.78. A very sheltered sandy beach facing west. Exposure scale 7. Samples collected from the north end of the beach at an isolated small boulder and pebble site.
8. *Porth Llanlana*, Anglesey. Grid Ref. SH387591. 3.2.78. A very sheltered boulder shore, facing north. Exposure scale 8. Samples collected from a transect of 20 metres down the shore.

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# SHELL SHAPE IN LIVING AND FOSSIL (NORWICH CRAG) *NUCELLA LAPILLUS* (L.) IN RELATION TO HABITAT

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**Abstract:** Shell shape has been examined in collections of fossil *Nucella lapillus* (L.) from the Norwich Crag (early Pleistocene), and compared with living populations from sites in the Firth of Forth, from the coast of Norfolk and elsewhere. Our samples of living North Sea populations show much less variation in relation to wave-exposure than Atlantic shells, and other factors can be involved. The rather tall and narrow fossil shells are appropriate for a sheltered or moderately sheltered site, such as a bay or firth or restricted sea, but caution must be exercised in such comparisons. The mechanism determining shell form is discussed.

## INTRODUCTION

The dogwhelk *Nucella lapillus* (L.) is found living between tide-marks, and occasionally below, on both sides of the cold-temperate North Atlantic and on North Sea coasts. Closely related shells, attributed to the same species, are found abundantly in early Pleistocene deposits in East Anglia. The purpose of this paper is to assess the relation of shell form with habitat in living *Nucella* and to explore the possibility that a knowledge of this may be used to deduce the environmental conditions of the fossil dogwhelks.

Populations of living *Nucella lapillus* vary greatly in shell shape, the maximum size of individuals, and the incidence of 'teeth' in the outer wall of the aperture. The shell is short and wide on an open Atlantic coast, but tall and narrow in sheltered places (Colton 1922, Moore 1936). The open-sea type has a larger foot, good for holding on in rough weather, while the sheltered type is more resistant to crabs (Kitching *et al.* 1966, Seed 1978, Hughes and Elner 1979). The fact that the eggs are laid within a capsule attached to the rock and hatch as miniature adults, so that there is no planktonic stage, makes it possible to suppose that adjoining local populations might have different genetic constitutions and thus might differ in shell shape. On the other hand local differences in environmental conditions such as food supply or disturbance by waves have also been considered as possible causes (Moore 1936, Spight 1973 for *Thais lamellosa* Gmelin). Dogwhelks reach a larger size in shelter than on the open coast (Ballantine 1961). Towards maturity the shell thickens, and 'teeth' often develop on the inside of the outer lip (Moore 1936). Interruption of feeding may also induce tooth formation (Crothers 1971). Thus tooth formation is associated with the continued deposition of calcium carbonate without corresponding growth of the body.

The fossil dogwhelks under consideration are from the Norwich Crag (early Pleistocene). They conform with Wood's (1848) *Purpura lapillus* var. *vulgaris*. The genus *Nucella* first appeared in the North Sea during the Pliocene. It is believed to have originated in the Pacific and to have entered the North Atlantic during a warm period when it was possible to pass around the Arctic Ocean. Such migrations have been described by Briggs (1970) and Strauch (1972). Forms resembling modern *Nucella lapillus* are found in the upper Red Crag and continued through the Norwich Crag. *Nucella* must have suffered drastic reduction in

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numbers, and was probably eliminated from the North Sea area, during successive glaciations. As the climate ameliorated in the Postglacial the North Sea could have been restocked from the north, even before the English Channel reopened. Interbreeding between two formerly separate stocks, after this connexion was reestablished, might even explain the chromosomal abnormalities found in *Nucella* on the coasts of Brittany (Staiger 1954) and southwest England (Bantock and Cockayne 1975). There can be little doubt that the tall narrow shells described by Crothers (1974) from the Bristol Channel represent a genetically distinct stock. Very considerable genetic differences are to be expected between preglacial and living populations. It is unlikely that any Crag *Nucella* is the direct ancestor of the living North Sea form. Great caution must be exercised in transferring ecological interpretations from the latter to the former.

In this paper we compare the shell characteristics of the fossil dogwhelks with those of living populations already described and of some additional living populations collected for this purpose. In view of similarities of the fossil shells with living shells from sheltered sites, a special survey was made by one of us (J.A.K.) of dogwhelks in the Firth of Forth, which offers a useful range of environmental conditions in a North Sea rather than an Atlantic situation.

#### SITES

Collections of living *Nucella lapillus* were made by J.A.K. at stations along the south side of the Firth of Forth from its mouth at Barns Ness and North Berwick up as far as the Forth Railway Bridge (Fig. 1). Isolated collections were also made from low littoral flint boulders on a gently sloping but fully open beach at West Runton, Norfolk, from a gently sloping beach of stones and mud at Weston-super-Mare on the Bristol Channel, and from a stony, gently sloping and very sheltered beach in Barloge Creek, near Lough Ine, Co. Cork. A collection was made from a sheltered very low littoral site with boulders covered with *Balanus crenatus* at Church Island in the Menai Strait by Dr. R. N. Hughes. Grid references are given in Table 1. All the collections were made indiscriminately and were large enough to embrace the full spread of shell sizes available but they may not represent precisely the size distribution of the whole population.

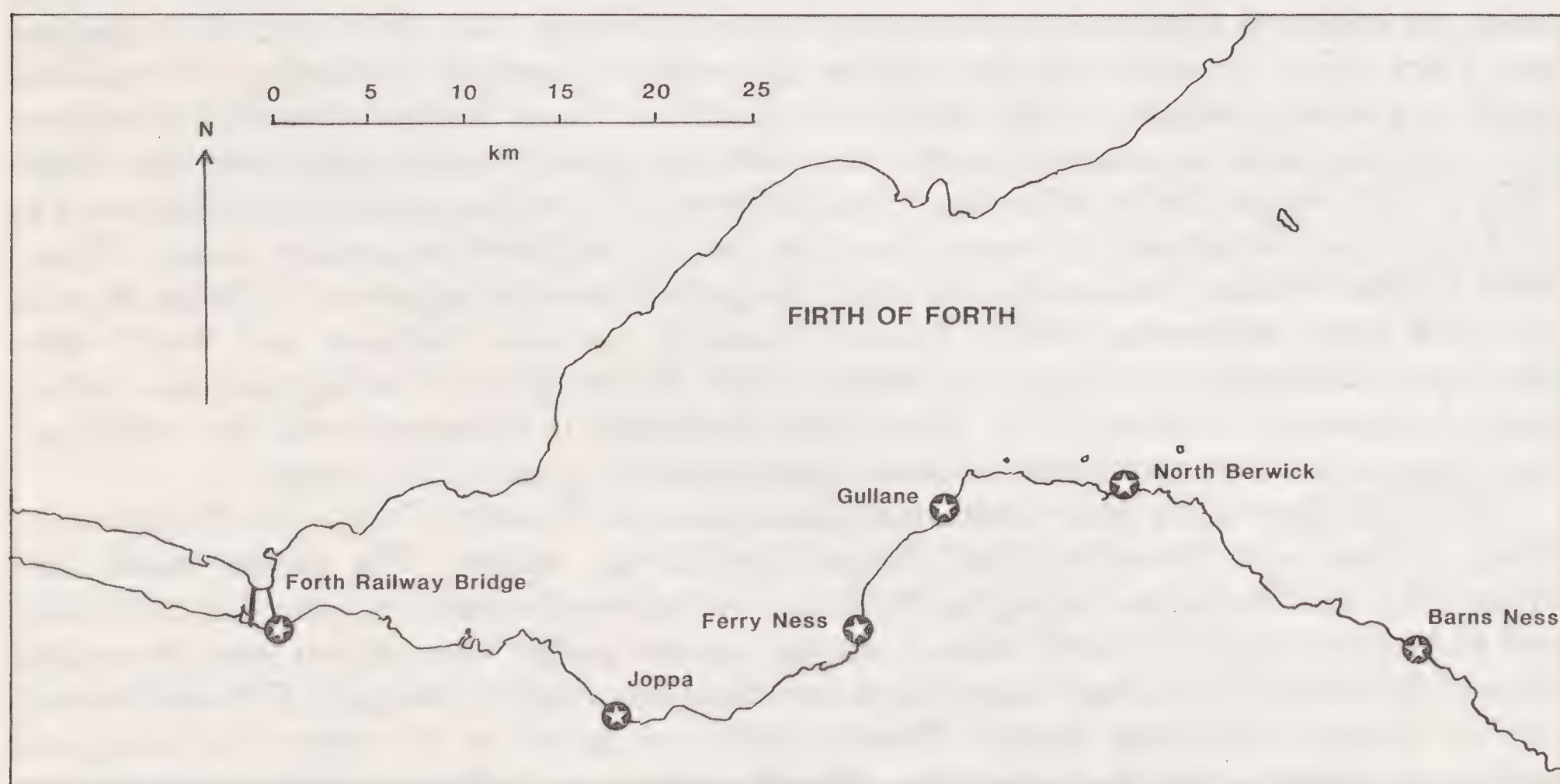


Fig. 1. Sites of collection of *Nucella lapillus* on the Firth of Forth.



We collected fossil *Nucella* from the Norwich Crag at Bramerton, Norfolk, and Wangford, Suffolk (see Fig. 1, Funnell *et al.* 1979). The Bramerton site is the upper shell bed in Blake's Pit. The Wangford site is on the 1969 section of West and Norton (1974) shown in their Fig. 7; we collected samples from the upper half and from the bottom of their section. Both at Bramerton and at Wangford the deposits contain much sand, with varying amounts of gravel and shells. In view of the evidence that many of these shells were transported before their ultimate deposition, these collections do not represent the original size distribution of the populations.

### SHELL MEASUREMENTS

The shells were numbered and the shell height and apical angle were measured, as well as two shell diameters one complete whorl apart, all as detailed in Fig. 3 and in accordance with previous procedure (Kitching 1977). Whorl ratio = the larger diameter/the smaller diameter. From apical angle and whorl ratio the spiral angle can be calculated (Moore 1936; this describes the steepness of the spiral within a specified cone; for full explanation see Thompson 1917). Shell shape changes with age, and therefore the measurements were designed to represent recent growth as far as possible. The data are presented as rectilinear regressions on shell height, or quadratic regressions if these give a significantly better fit, extending in each case only over the range of height classes represented in the collection.

### RESULTS

The distribution of shell heights in the collections and the occurrence of teeth in the various height classes are given in Fig. 2, and regressions for shell shape at the more important stations in Fig. 3. Table 1 gives estimates of whole ratio, apical angle and spiral angle for a shell height of 25 mm, with their standard errors, for all the collections; it also gives information about the available supply of food for dogwhelks.

### DISCUSSION

*Shell size.* Within our experience *Nucella lapillus* does not reach a large size at sites fully open to severe wave action. No shells exceeded 30 mm in height in samples from the open coast in south-west Ireland, north Scotland or Galicia, whereas substantial numbers exceeded this height at adjacent sheltered sites (Kitching 1977). Shells reached the 37.6–40.0 mm height class on mussel beds in the firths of Galicia, where food is easily accessible and unlimited in quantity. In the present investigation the largest sizes were again attained at sheltered sites with a plentiful supply of food: Church Island in the Menai Strait and Ferry Ness, Joppa and the Forth Railway Bridge on the Firth of Forth. Very large *Nucella* have been reported by Cole (1956) to destroy oyster spat in Essex estuaries. Some very large shells (50–60 mm) are reported from sublittoral sites off Minehead and Swanage, from depths sufficient to protect them from wave action (Moore 1936). Very tall and narrow shells are found on the Somerset coast of the Bristol Channel, at sites of moderate wave-exposure or shelter (Crothers 1974). A few of the *Nucella* from all three fossil collections far outstrip in shell height all living shells we have taken from open Atlantic sites. Their large size appears to be incompatible with full exposure to oceanic waves, and accords best with a geographically sheltered situation, although it remains possible that either a sublittoral site or a boulder-strewn beach in a bay or sea of restricted size might provide the necessary shelter.

*Shell shape.* Shell shape changes as the shell grows: both the whorl ratio and the apical angle decrease towards maturity. Nevertheless on Atlantic coasts of the British Isles the values of



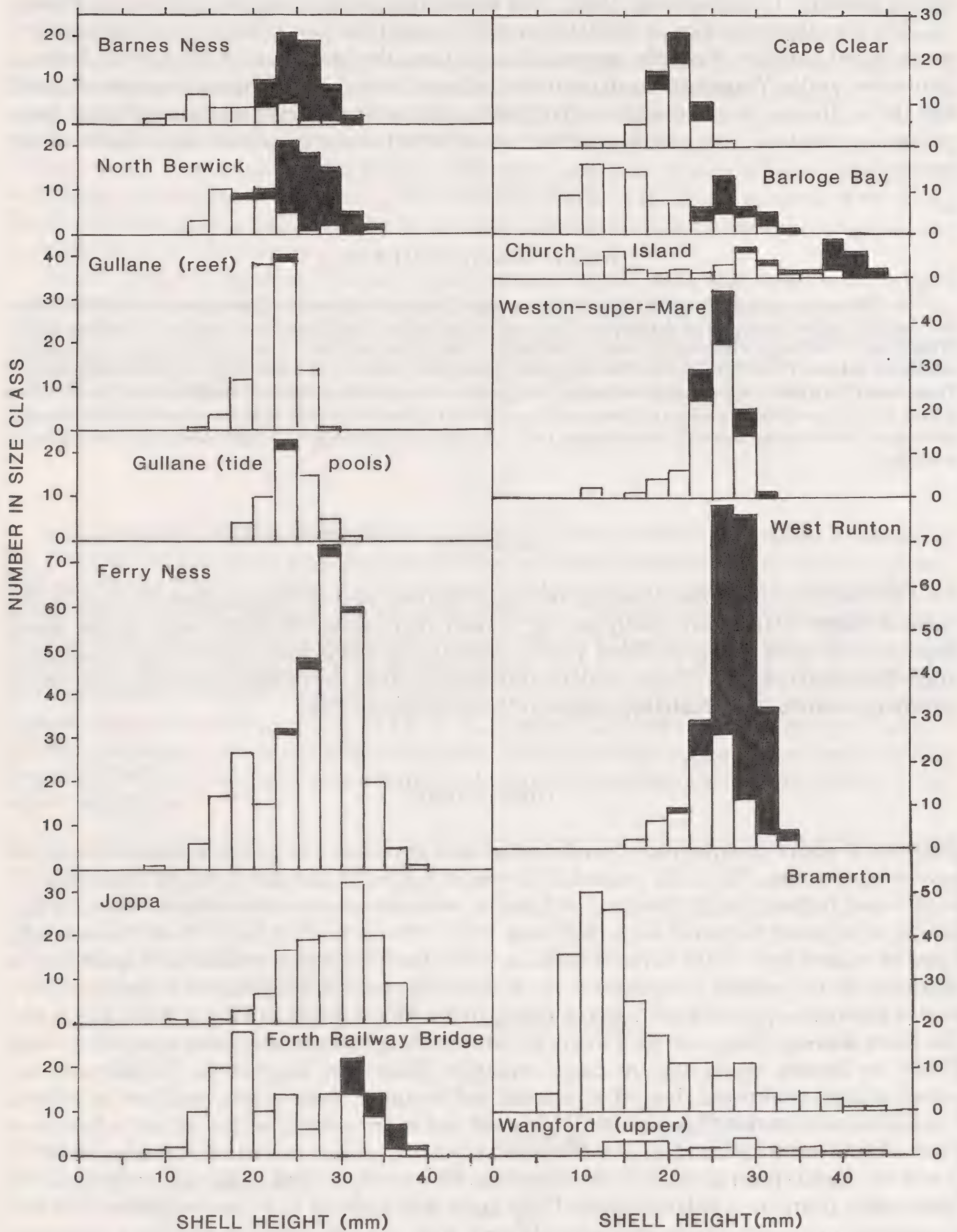


Fig. 2. Frequency distributions of shell height in the collections of *Nucella lapillus*. Solid black indicates numbers with teeth in the outer lip of the aperture. The data from Clear Island are from Kitching (1977).



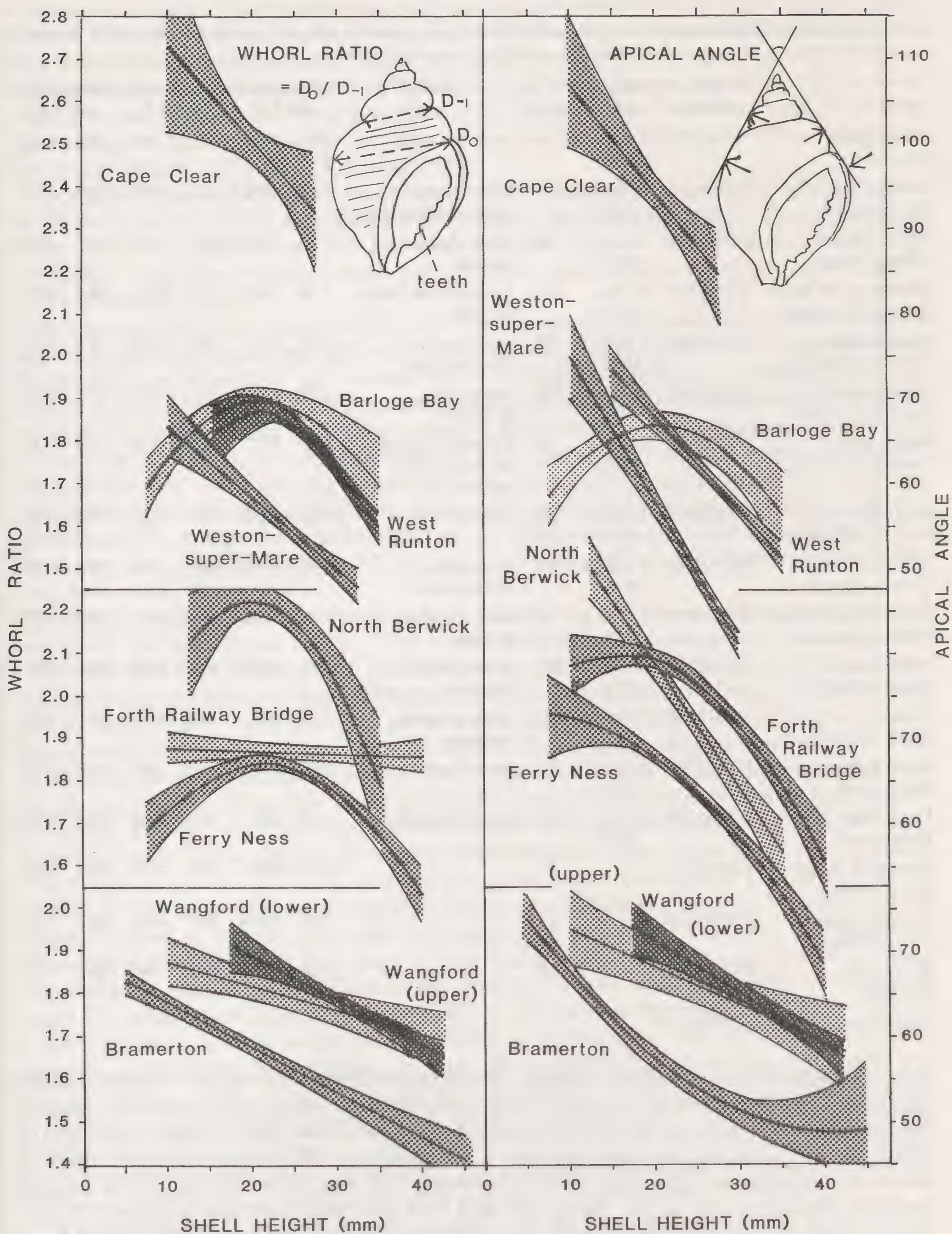


Fig. 3. Regressions of whorl ratio and apical angle on shell height for *Nucella lapillus*. Shading marks  $2 \times$  standard error on either side of regression line. The data from Clear Island are from Kitching (1977).



TABLE 1

Sites of collection of *Nucella lapillus*, and estimates of whorl ratio, apical angle and spiral angle for a shell 25 mm in height, with their standard errors.

Site	grid reference	date coll.	no. of shells	food at site	whorl ratio and S.E.	apical angle and S.E.	spiral angle and S.E.
*Cape Clear (Co. Cork)	V942198	6 July 1970	61	many mussels	2.39 0.05	87.9 1.97	78.7 0.19
Barloge Bay (C. Cork)	W100274	19 July 1977	101	a few barnacles, some <i>Littorina</i> spp.	1.88 0.02	65.7 0.89	79.6 0.12
Church Island (Menai Strait)	SH552716	July 1979	50	many <i>Balanus crenatus</i>	1.83 0.02	64.9 0.83	79.8 0.14
Weston-super-Mare (Bristol Channel)	ST317614	14 Dec. 1977	110	barnacles on stones on mud	1.58 0.007	49.5 0.45	80.0 0.08
West Runton (coll. 1) (Norfolk)	TG187437	7 Feb. 1973	92	barnacles on flint boulders	1.87 0.01	64.0 0.62	79.4 0.11
West Runton (coll. 2) (Norfolk)	TG187437	11 Oct. 1980	239	same site as above	1.84 0.008	62.4 0.44	79.5 0.07
Barns Ness (mouth of Forth)	NT725770	27 Dec. 1976	80	barnacles on rocks on beach; no mussels	2.00 0.02	68.1 0.68	78.9 0.13
North Berwick (mouth of Forth)	NT558855	3 Oct. 1977	91	mussel beds	2.18 0.02	71.6 0.67	78.2 0.09
Gullane (reef) (Firth of Forth)	NT470830	5 Oct. 1977	110	mussels on vertical face	2.01 0.02	68.6 0.69	78.8 0.10
Gullane (tide pools) (Firth of Forth)	NT470830	5 Oct. 1977	59	many mussels in pools	1.91 0.02	64.4 0.67	79.0 0.11
Ferry Ness (Firth of Forth)	NT435775	1 Oct. 1977	307	mussel beds; barnacles on rocks	1.83 0.007	63.7 0.39	79.6 0.06
Joppa (Firth of Forth)	NT313738	27 Dec. 1977	130	many mussels, barnacles	1.90 0.01	71.2 0.51	80.0 0.08
Forth Railway Bridge (coll. 1)	NT137785	23 Dec. 1978	77	many barnacles	2.01 0.03	78.3 1.30	80.0 0.15
Forth Railway Bridge (coll. 2)	NT135784	20 Oct. 1980	150	many barnacles	1.87 0.01	76.5 0.69	80.3 0.13
Wangford (upper site) (Suffolk)	TM464779	—	27	—	1.79 0.015	66.2 1.16	80.2 0.10
Wangford (lower site) (Suffolk)	TM464779	—	73	—	1.84 0.016	68.4 0.98	80.7 0.09
Bramerton (Norfolk)	TG298061	—	235	—	1.62 0.012	62.0 0.86	80.4 0.12

\*collection of Kitching (1977).

these characteristics are strikingly higher – for corresponding shell heights – at wave-exposed sites than in shelter. Even on fully open North Sea shores the apical angle and whorl ratio do not reach the high values of the open Atlantic. Dogwhelks of the open Atlantic must hold on tightly to the substrate for long periods – a requirement which might operate either by selection of appropriate genotypes or by influencing shell deposition directly. Wave action is probably less persistent in the North Sea and therefore may exert less influence. Higher values of whorl ratio and apical angle are attained on the open mussel beds at Filey Brigg (Kitching 1977) and North Berwick (Fig. 3) than at sheltered sites in the Firth of Forth up to Ferry Ness. However, at the Forth Railway Bridge, at a site so sheltered that the shell



sculpture is unusually fresh, the apical angle of the larger shells is even higher than at North Berwick. Factors other than wave action seem to be involved. Crothers (1979) has reported a lack of correlation between wave action and shell shape in the Shetland Islands. Our two collections from the fully open coast at West Runton (Norfolk) show a consistently low apical angle, but flint boulders and the gentle slope of the shore must provide some local protection. *Thais emarginata* Deshayes was also found to have a lower apical angle on open boulder-strewn beaches in British Columbia (Kitching 1976).

Wangford dogwhelks overlap in shell shape with living populations at sheltered sites, and the Bramerton specimens approach those living at Weston-super-Mare. Nevertheless in living North Sea populations the variation in shell shape is limited and not yet fully predictable. The shape of fossil shells must be interpreted with caution, but is compatible with a sheltered habitat.

*Teeth.* Our results for the Forth area (Fig. 2) show a much greater incidence of teeth at the two wave-exposed sites (including the mussel bed at North Berwick) than in shelter. However, the development of teeth is not confined to wave-exposed situations. At Barloge Bay, Co. Cork, a sheltered station with very limited food supply, over half the specimens exceeding 25 mm in height had teeth. We do not know whether different environmental conditions, such as temperature or salinity, may not have reduced the tendency to form teeth in the fossil *Nucella*, nor whether this tendency was genetically less strong. Thus tooth formation is for our purposes an uncertain guide. However, the nearest approach to the complete lack of teeth in the Norwich Crag material is to be found in the collections from mussel beds in shelter (at Joppa and Ferry Ness in the Firth of Forth and in the firths of Galicia), where specimens with teeth are scarce.

*Other fossils.* The fossil molluscs found in the Norwich Crag at Bramerton have been surveyed extensively by Funnell *et al.* (1979). They include littoral and sublittoral species, and species associated with hard and with soft substrates. Mussels (*Mytilus edulis* L.), winkles (*Littorina* spp.), and also the barnacle *Balanus crenatus*, of which there are many plates, are all potential food for dogwhelks. Some barnacle plates and some *Littorina* shells have drill holes. The diversity of habitats normally occupied by all these fossil shells indicates that they have been moved from their original sites (Norton 1967). Thus neither the assemblage of fossil species nor the distribution of particle size can indicate precisely the habitat of the fossil *Nucella*.

*Conclusions.* Even at fully wave-exposed North Sea stations in Scotland or England, the shells of *Nucella lapillus* do not approach the short wide-mouthed form found on an open Atlantic coast (Cape Clear in Fig. 3). On such a coast there is an abundance of food in the form of mussels, but ocean swell persists long after a storm and dogwhelks must hold on tightly to the substrate. Even if Atlantic and east coast stocks are genetically different, we suspect an environmental influence on shell form. A combination of rapid early growth with a widely extended foot and mantle might lead to the deposition of new shell subtending a wide apical angle. The progressive changes in apical angle of populations depicted in Fig. 3 are reflected in the curvature of shell profile in the individual dogwhelks. They are a feature of their ontogeny, and cannot be explained by selection acting upon individuals of different but constant apical angle. Increase in apical angle during early growth, as seen in some populations, might perhaps result from a change in microhabitat affecting shelter or food supply. The universal decrease in this angle during later life is probably associated with a decreasing specific growth rate of the body but continued deposition of calcium carbonate. These suggestions would explain the wide diversity of shell form at different sites.

It is unlikely that dogwhelks as tall and narrow as the fossil specimens could have endured the wave action of an open Atlantic coast, although they might have withstood moderate wave-exposure on an open beach giving local shelter in the form of crevices or boulders. The lack of teeth might indicate – very uncertainly – a plentiful supply of food. The most probable



habitat of the fossil *Nucella* is on the low littoral of a restricted bay or firth. This accords with the general conclusions of Funnell *et al.* (1979) about conditions at that time.

## ACKNOWLEDGEMENTS

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## DESCRIPTION D'ESPÈCES ABYSSALES DE NUCULACEA DES AÇORES†

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**Abstract:** In this paper the author describes two new species of marine bivalve molluscs, *Nucula aureliae* and *Nuculana foresti*, collected by dredging from a depth of 3360 m in the Azores archipelago, to the west of the island of Flores, during the oceanographic trip 'Biaçores' made on the oceanographic ship Jean Charcot. These new species differ from the known species, for *Nucula aureliae* by its shape, the convexity of its valves, the thickness of the shell, the shape and the place of the umbo and the measure of the angle of it, and for *Nuculana foresti* by the shape and the dimensions of its strong shell, its inflated and projecting beaks, its rounded valves with a regular sculpture and its wide hinge.

**Résumé:** L'auteur décrit dans cet article deux nouvelles espèces de mollusques lamellibranches marins, *Nucula aureliae* et *Nuculana foresti*, recueillies par dragage à 3360 m de profondeur dans l'archipel des Açores, à l'ouest de l'île de Flores, lors de la campagne océanographique 'Biaçores' du navire océanographique Jean Charcot. Ces espèces nouvelles diffèrent des espèces connues, pour *Nucula aureliae* par sa forme générale, la convexité de ses valves, l'épaisseur de sa coquille, la forme et la position de l'umbo et la valeur de l'angle au sommet, et pour *Nuculana foresti* par la forme et les proportions de sa coquille solide, ses crochets renflés et saillants, ses valves bombées à sculpture régulière et son large plateau cardinal.

Au cours de l'étude des lamellibranches récoltés lors de la campagne océanographique Biaçores du navire océanographique Jean Charcot, campagne du Muséum National d'Histoire Naturelle de Paris qui s'est déroulée du 29 Septembre au 20 Novembre 1971, principalement dans l'archipel des Açores, j'ai rencontré plusieurs échantillons de Nuculacea appartenant à deux espèces nouvelles dont la description fait l'objet de cet article. Les holotypes et les paratypes de ces deux espèces sont conservés dans les collections du Muséum National d'Histoire Naturelle, Paris.

### ***Nucula aureliae* n. sp.**

#### *Description de l'holotype.*

La coquille est solide, équivalve, presque aussi haute que longue, inéquilatérale, la partie post-umbonale occupant 33% de la longueur totale. Les valves sont relativement peu épaisses et recouvertes par un périostracum beige-jaunâtre, brillant, plus foncé et légèrement brunâtre près du bord dorsal antérieur et postérieur et près de l'extrémité antérieure. Ces valves sont treillissées extérieurement par des côtes concentriques de croissance, fines, arrondies, peu régulières et par des côtes rayonnantes aussi fines ou légèrement plus fortes mais plus régulières. Ces côtes rayonnantes sont absentes aux deux extrémités des valves dans la région comprise entre le bord dorsal et la côte rayonnante passant par le point de jonction de la troncature des extrémités antérieure et postérieure avec le bord ventral. Le bord dorsal antérieur est rectiligne tandis que le postérieur, beaucoup plus court, est concave à l'emplacement de la charnière, puis sub-convexe et pratiquement rectiligne ensuite. Le bord ventral qui est ébrèché sur une assez grande étendue de sa longueur, est convexe et très

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finement crénelé. Les sommets situés dans la moitié postérieure de la coquille, proéminents, légèrement dirigés vers l'arrière, sont dépourvus de périostracum et d'un blanc terne. La lunule qui occupe la quasi totalité de la partie postérieure dépourvue de sculpture, est allongée et ventrue, limitée par un sillon très faiblement marqué qui va du crochet au bord dorsal postérieur un peu au dessus de l'angle postéro-ventral. Cette lunule, d'une couleur un peu plus foncée que le reste de la coquille, est concave près du crochet dans la région correspondant à la partie postérieure du plateau cardinal, puis légèrement convexe ensuite. L'aréa ligamentaire, lancéolée, s'étend du crochet à l'angle antéro-dorsal, et n'est séparée du reste de la coquille que par sa couleur un peu plus foncée. La surface interne des valves est nacrée et ornée sur sa totalité, à l'exception des extrémités, par les empreintes fines, régulières et serrées, des stries rayonnantes. Les impressions des muscles adducteurs sont peu marquées. L'impression antérieure est allongée, phaséolée; la postérieure est ovale et quelque peu plus petite que l'antérieure. La ligne palléale, faiblement marquée est entière. Le ligament amphidète, assez long n'est que faiblement développé. Le plateau cardinal très étroit et sinueux, coudé, supporte des dents minces et pointues au nombre de dix sept vers l'avant et de neuf vers l'arrière. A l'emplacement du coude du plateau cardinal, séparant les parties antérieure et postérieure de la charnière, se trouve un petit résilifer sous-umbonal, de forme triangulaire, faisant une saillie antéro-ventrale dans le profil du plateau cardinal. Ce résilifer supporte un résilium bien développé.

#### *Parties molles.*

Le pied qui est très développé représente la moitié du corps de l'animal; son bord libre est dentelé.

#### *Dimensions de l'holotype:*

longueur 8,4, hauteur 7,0, épaisseur 2,0 mm; nombre de dents (N.d) antérieur 17, postérieur 9.

#### *Provenance de l'holotype*

L'holotype a été recueilli vivant par dragage lors de la campagne océanographique 'Biaçores' (1971) du N. O. 'Jean Charcot' à la station 126 (39° 19,5' lat. N, 33° 47' long. W, c'est-à-dire à l'ouest de Flores) par 3360 m de profondeur, le 23 Octobre 1971 à 07 h 30 (heure locale), à l'aide d'une drague traîneau épibenthique de Sanders, sur un fond de vase à globigérines.

#### *Paratypes*

A cette même station ont été recueillis vivants cinq autres spécimens et une valve droite de *Nucula aureliae*. Leurs dimensions (mm), nombre de dents (No d) et rapports de la longueur de la partie post-umbonale à la longueur totale (Pu), sont les suivants:

longueur	hauteur	épaisseur	ant.	nombre de dents (No d)		Pu%
8,2 (VD)	6,7	1,5 (VD)	—	—	—	33,3= $\frac{1}{3}$
5,0	4,4	2,6	13	7		33,0
4,3	3,7	2,1	11	6		32,5
4,1	3,5	2,1	11	7		31,7
4,0	3,4	2,2	10	VG: 3		32,5
				VD: 1*+3+1*		
3,3	2,8	1,9	9	5		33,3= $\frac{1}{3}$

VD: valve droite; VG: valve gauche; \*: dents très petites, avortées.



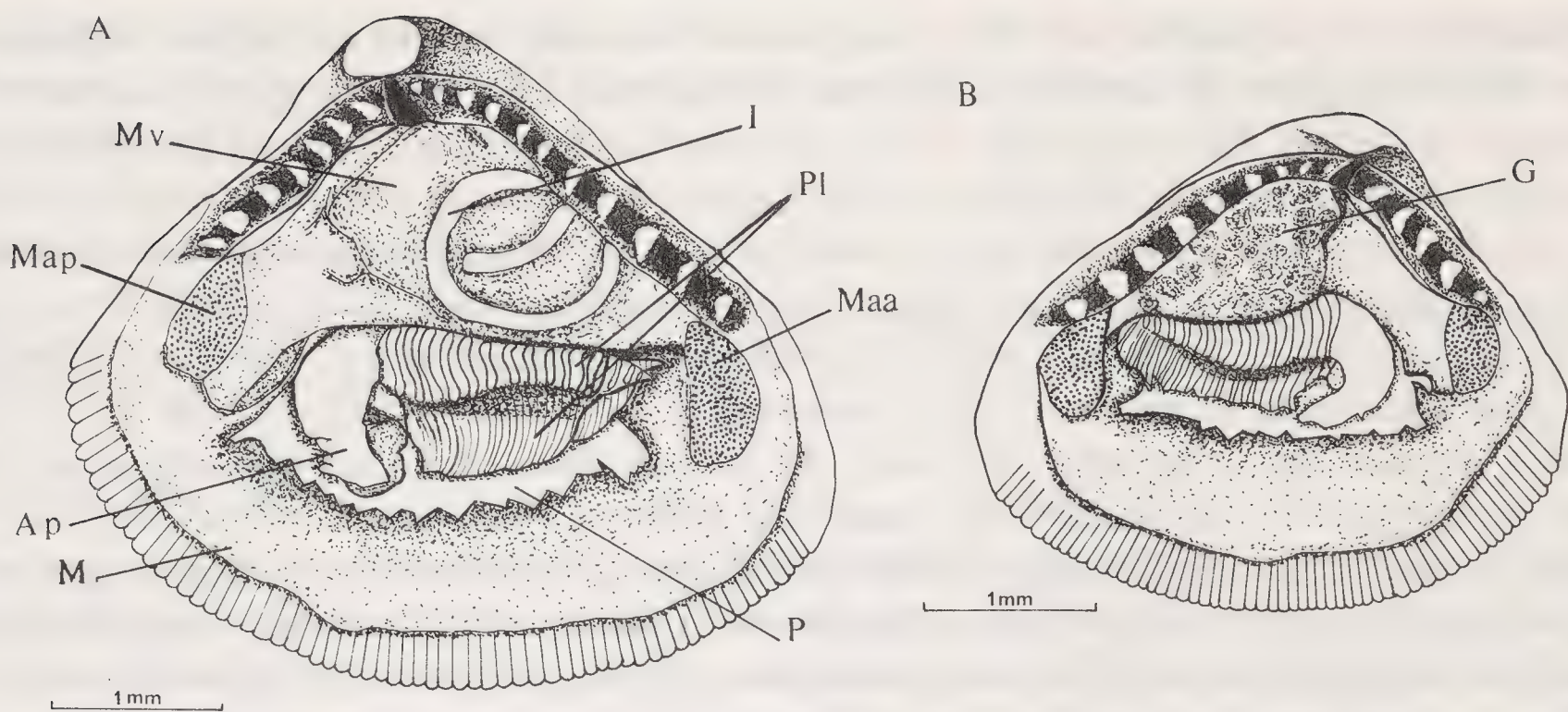


Fig. 1. *Nucula aureliae* n. sp., paratypes. A). animal vu du côté droit, le lobe palléal étant enlevé. B). animal vu du côté gauche, le lobe palléal étant enlevé. Ap: appendice postérieur issu du bord dorsal commun des palpes. G: glande génitale. I: intestin. M: manteau. Maa: muscle adducteur antérieur. Map: muscle adducteur postérieur. Mv: masse viscérale. P: pied. Pl: palpes labiaux.

Tous les paratypes sont bien semblables à l'holotype et ne présentent que de très légères différences avec ce dernier.

Ils ont tous une forme comparable avec celui-ci, mais ils sont un peu plus haut par rapport à leur longueur, sauf chez le paratype qui n'est constitué que par une valve droite. Cette valve qui a des dimensions un peu inférieures à celles de l'holotype, est en mauvais état, le crochet est très érodé et le plateau cardinal ainsi que la charnière ont presque totalement disparu. Tous les paratypes ont les sommets, sur une surface plus ou moins grande, dépourvus de périostracum et sont comme l'holotype, dans cette région, d'un blanc terne.

La lunule est légèrement concave près des crochets, ou sub-convexe, et nettement convexe et proéminente ensuite. En liaison avec la lunule les crochets ne sont pas aussi saillants et ne sont pas aussi recourbés vers l'arrière que chez l'holotype. Le plus petit des paratypes a une forme un peu plus massive, des sommets plus larges et des côtes rayonnantes difficilement perceptibles alors que les côtes de croissance concentriques sont plus marquées et légèrement variqueuses. Celui dont la longueur est de 4,0 mm possède une lunule et une aréa ligamentaire qui sont peu nettement limitées, des côtes de croissance irrégulières qui sont plus visibles que les côtes rayonnantes et plus aiguës. Sa lunule légèrement convexe près du crochet est brusquement creusée par une rentrée assez profonde qui semble être le résultat d'un accident, avec arrêt de croissance à l'endroit touché, puis normalement convexe ensuite. A cette rentrée de la lunule vers l'intérieur, correspond sur le plateau cardinal une charnière réduite composée de trois dents seulement dans la valve gauche, et dans la valve droite de trois dents avec de part et d'autre une petite protubérance qui semble être une dent avortée. Enfin, le nombre de dents de la charnière est variable d'un échantillon à l'autre et il est en relation étroite avec la taille de la coquille; le plus petit nombre étant observé chez le plus petit paratype de 3,3 mm de long (exception faite du paratype de 4,0 mm de long qui est anormal) et le plus grand nombre chez le plus grand spécimen, qui est l'holotype de l'espèce.

#### *Rapports et différences*

*Nucula aureliae* présente des rapports par sa sculpture treillissée par des côtes de croissance concentriques et par des côtes rayonnantes qui vont de l'umbo au bord ventral, et par son bord ventral crénelé avec *Nucula nucleus* (L.), *N. turgida* Leckenby et Marshall, *N. hanleyi*



Winckworth et *N. sulcata* Bronn. Ses valves sont recouvertes par un périostracum brillant comme chez *N. turgida*, *N. hanleyi*, et *N. tenuis* (Montagu) Elle possède quelque ressemblance par sa forme générale, bien que celle-ci soit un peu plus haute par rapport à la longueur, avec les nœuds cités ci-dessus, mais elle s'en distingue par un bord dorsal antérieur qui est plus long et rectiligne jusqu'à l'umbo qui est bien plus large et proéminent et moins incliné vers l'arrière, ce qui accentue encore la concavité du bord dorsal postérieur. Elle diffère aussi de *N. nucleus* et *N. hanleyi* par l'angle au sommet, formé par les bords dorsaux antérieur et postérieur, qui est plus aigu et de *N. nucleus* et de *N. sulcata* par une coquille qui est bien moins épaisse.

*Nucula aureliae* est à rapprocher aussi de *N. atacellana* Schenck (*nomen novum* pour *N. reticulata* Jeffreys 1876 *non* Hinds = *N. cancellata* Jeffreys 1881 *non* Meck et Hayden) par sa sculpture décussée qui est cependant plus fine et bien plus nettement marquée, par son bord ventral crénelé et par ses bords dorsaux antérieur et postérieur tronqués à leur extrémité. Elle s'en éloigne surtout par sa taille beaucoup plus grande, par sa forme générale plate et non arrondie, son crochet plus étroit et plus saillant situé dans la moitié postérieure de la coquille, par son extrémité antérieure plus proéminente et son bord ventral dont le rayon de courbure est beaucoup plus grand.

Aucune des autres espèces abyssales mentionnées par Clarke (1962, p. 47–49) n'est comparable à notre espèce, tout au moins en ce qui concerne la forme qui est vraiment très différente.

Je tiens à remercier particulièrement le Dr. Harald A. Rehder, de la Smithsonian Institution, qui a eu la grande amabilité de m'envoyer en prêt des échantillons de *Nucula reticulata* Jeffreys, de la collection Jeffreys, qui est conservée dans ce musée, des expéditions du 'Porcupine' (1869) et du 'Valourous' (1875); le lectotype et deux paralectotypes de la *Nucula atacellana* de Schenck (coll. Jeffreys, expéd. du 'Porcupine'); les deux spécimens des Açores de l'expédition du 'Challenger' (malheureusement brisés) déterminés par Jeffreys et publiés par E. A. Smith; ainsi que de nombreux échantillons de *N. cancellata* étudiés par Verrill. Tous ces matériaux nous ont permis de pouvoir les comparer avec notre espèce.

Cette espèce nouvelle est dédiée à ma fille Aurélia.

### ***Nuculana foresti* n. sp.**

#### *Description de l'holotype*

Coquille solide, équivalve, subéquilatérale, légèrement plus allongée vers l'arrière (la partie post-umbonale occupe 55–56% de la longueur totale), d'un blanc terne, ornée de très nombreuses côtes concentriques régulières sur toute la surface externe, à peine visibles à l'œil nu, séparées par des espaces qui sont un peu à presque deux fois plus larges qu'elles. Ces côtes se renforcent en allant de la région apicale vers le bord ventral et s'amincissent en se rapprochant les unes des autres vers les deux extrémités des valves, de sorte que les espaces qui les séparent sont considérablement réduits et ne sont plus dans ces régions que d'une largeur équivalente à celle d'une côte. Bord dorsal antérieur concave près du crochet, et convexe ensuite, beaucoup plus court que le postérieur qui est déclive, rectiligne et subrostré. Bord ventral convexe et non crénelé. Sommets situés dans la moitié antérieure de la coquille, saillants, légèrement inclinés vers l'arrière. Lunule ovale, concave, petite et bien marquée; aréa ligamentaire étroite, allongée, de forme ovale acuminée aux deux extrémités non distinctement limitée. Intérieur des valves luisant. Impressions des muscles adducteurs des valves peu visibles; celle du muscle adducteur antérieur est beaucoup plus grande que celle du muscle adducteur postérieur. La ligne palléale peu visible, est assez profondément échancrée par l'empreinte du sinus palléal. Le plateau cardinal sinueux, rectiligne sous le crochet sur une longueur de 0,6 mm, assez large par rapport aux dimensions des valves, porte une charnière coudée, composée, de part et d'autre d'un petit résilifer, ou cuilleron ligamentaire sous-umbonal qui supporte la couche interne du ligament, vers l'avant, de sept



dents fortes et saillantes et près du crochet de quatre dents petites et peu saillantes; vers l'arrière de cinq dents petites et peu saillantes près du crochet et de neuf dents fortes et très saillantes plus en arrière.

*Dimensions de l'holotype:*

longueur 5,8, hauteur 4,7, épaisseur 1,7 mm (1 valve); nombre de dents (N.d), antérieur (7+4), postérieur (5+9).

*Provenance de l'holotype*

L'holotype a été récolté mort par dragage par le N. O. 'Jean Charcot' lors de la campagne océanographique 'Biaçores' à la station 126 (39° 19,5' lat. N, 33° 47' long. W, c'est-à-dire à l'ouest de l'île de Flores) par 3360 m de profondeur, le 23 Octobre 1971 à 07 h 30 (heure locale) à l'aide d'une drague traîneau épibenthique de Sanders, sur un fond de vase à globigérines.

*Paratype.*

A cette même station a été recueilli mort également, un second échantillon, plus petit, dont les dimensions sont les suivantes:

longueur 3,6, hauteur 2,6, épaisseur 1,2 mm (1 valve); nombre de dents (N. d), antérieur (6+4), postérieur (4+7).

Cet échantillon, très semblable à l'holotype, ne présente avec celui-ci que de très légères différences. La coquille est un peu plus équilatérale (la partie post-umbonale n'occupe que 52% de la longueur totale de la coquille), les crochets sont quasi médians et un peu plus saillants; le côté antérieur est à peine concave près du sommet et le côté postérieur est d'une rectitude moins nette et d'une déclivité plus faible. La charnière n'est composée vers l'avant que de six dents fortes et saillantes et près du crochet de quatre dents petites et peu saillantes; vers l'arrière, de quatre dents petites et peu saillantes près du crochet et de sept dents fortes et saillantes plus en arrière.

*Rapports et différences*

Cette espèce s'apparente surtout par la sculpture aux échantillons décrits et figurés par Locard (1898, p. 348, pl. 14, fig. 19-21) sous le nom de *Leda pusio* Philippi. Elle en diffère par sa coquille plus solide, moins haute et en proportion plus allongée, par ses crochets plus renflés et plus saillants, par ses valves plus bombées et son extrémité postérieure qui semble tronquée en comparaison de celle de *L. pusio* qui est plus étroite et moins convexe, ainsi que par son plateau cardinal plus large et plus sinueux.

Sa forme quasi équilatérale, ses sommets médians, son côté postérieur à peine allongé et subrostré ainsi que sa sculpture rapprochent *Nuculana foresti* de *Nuculana alluaudi* (Dautzenberg et H. Fischer). Elle s'en distingue, par contre, par ses crochets plus saillants, sa sculpture bien plus régulière, son simili rostre bien marqué, son bord dorsal antérieur concave et sa charnière plus large.

Enfin, *Nuculana foresti* est comparable à *Nuculana mirmidina* (Dautzenberg et H. Fischer) par sa sculpture qui est composée de stries d'accroissement très fines dans la région apicale, plus fortes et plus espacées vers le bord ventral, mais elle en diffère par sa forme plus équilatérale, par son bord dorsal antérieur concave et son bord dorsal postérieur rectiligne, par son crochet quasi médian, son bord ventral plus régulièrement convexe, par son extrémité postérieure moins arrondie et par sa hauteur plus grande par rapport à sa longueur.



Cette espèce a été nommée en l'honneur de Monsieur le Professeur J. Forest, chef de la mission 'Biaçores'.

## REMERCIEMENTS

Je remercie Mr le Professeur J. Forest, Muséum National d'Histoire Naturelle, Paris, chef de la mission 'Biaçores', qui m'a accueilli à bord du N. O. 'Jean Charcot' comme membre participant et qui a bien voulu me confier l'étude des bivalves, le Dr. H. A. Rehder, Smithsonian Institution, Washington, pour le prêt de matériaux de la collection Jeffreys conservée à la Smithsonian Institution, ainsi que Mr. le Professeur J. A. Allen qui a bien voulu lire et critiquer ce travail. Je remercie également Madame Guillaumin pour les photographies prises à l'aide du microscope électronique à balayage Cameca du Laboratoire d'Evolution des Êtres Organisés de l'Université Pierre et Marie Curie et Monsieur A. Foubert de notre laboratoire pour la réalisation des autres clichés.

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## PLANCHE 1 (opposite).

Fig. 1-2. *Nucula aureliae* n. sp., holotype, ×5. Fig. 3. *N. aureliae* n. sp., paratype 4,0×3,4 mm, ×10. Fig. 4-5. *Nuculana foresti* n. sp., holotype, ×8. Fig. 6. *N. foresti*, paratype, ×10. Fig. 7. *N. aureliae*, paratype, 4,1×3,5 mm, détail de la sculpture, ×300. Fig. 8. *N. aureliae*, paratype 3,3×2,8 mm, valve gauche, ×84. Fig. 9. *N. aureliae*, paratype 4,1×3,5 mm, valve droite, ×30. Fig. 10. *Nuculana foresti*, paratype, détail de la sculpture, ×300. Fig. 11. *N. foresti*, paratype, valve gauche, ×30. Fig. 12. *N. foresti*, paratype, valve droite, ×112. (Figs. 7-12 photographies au microscope électronique à balayage Cameca).







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# THE DISTRIBUTION OF SPHAERIIDAE IN RIVERS AND STREAMS OF CENTRAL SOUTHERN ENGLAND

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*Abstract:* Collections of Sphaeriidae from 124 sites on rivers and streams in central southern England yielded two *Sphaerium* and eleven *Pisidium* species. *P. casertanum* and *P. personatum* were recorded most frequently from the intermittent headwaters, while *S. lacustre*, *S. corneum*, *P. henslowanum* and *P. hibernicum* showed a preference for sites with a channel width exceeding 25 m. An analysis of association between species indicated two groupings. One group (*P. amnicum*–*P. henslowanum*–*S. lacustre*–*P. hibernicum*) had a linear structure; the other (*P. subtruncatum*–*P. personatum*–*P. milium*–*P. nitidum*–*P. pulchellum*) had more between-species associations.

## INTRODUCTION

The present study describes the patterns of distribution of the Sphaeriidae from flowing water sites within some of the river catchments in central southern England. Bishop & Hewitt (1976) give detailed distributions of *Pisidium* spp in eastern England and Kerney (1976) illustrates distribution records for all species of Sphaeriidae up to 1976, on a 10 km square system. In mainland Europe the lower reaches of the rivers Rhine, Meuse and Scheldt were studied by Kuiper & Wolff (1970), many species being common to the present survey. Meier-Brook (1975) has described the distribution of *Pisidium* spp in central Europe. He has suggested an ecological indicator value for each species but states that abundance rather than presence of a species must be taken into account. In this study quantitative sampling was not attempted because of the degree of sample replication required to overcome the effects of variable population densities. Effort was concentrated on visiting a large number of sampling sites.

## DESCRIPTION OF SAMPLING SITES

The rivers included in the survey are indicated in fig. 1. Much of the area is calcareous and all the rivers have a high proportion of ground water from chalk or limestone aquifers contributing to their flow. Some of the tributaries of the lower reaches of the R. Stour drain tertiary gravels. The R. Stour also receives drainage from the Blackmore Vale, an area of predominantly clay soils, but levels of calcium and pH are generally high at all the sampling sites. The water chemistry of some of the catchments has been described in detail by Casey & Newton (1973) (R. Frome), Hansford (1978) (R. Stour), Ham *et al.* (1982) (R. Lambourn), Mackey *et al.* (in prep.) (R. Coln) and Mackey *et al.* (in prep.) (R. Test, R. Itchen, R. Meon).

The headwaters of chalk streams are typically intermittent in flow and 13 sites included in the survey were in the intermittent section of the rivers. Many sites had a high cover of macrophytes, *Ranunculus* spp often being dominant but with *Berula erecta* (Hudson) Coville

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Fig. 1. Map of central southern England showing the location of the river systems sampled during the survey.

and *Callitriche* spp also well represented. At sites with intermittent flow *Apium nodiflorum* (L.) Lag and *Nasturtium officinale* R. Br. were more commonly recorded.

#### METHODS

Preliminary sampling established that few sphaeriids occurred below the top 20–30 mm of the substratum. It was therefore considered adequate to collect sediment samples by skimming the surface with either a soil sieve (0.5 mm mesh size) or a long-handled pond net (0.9 mm mesh size). The samples were taken back to the laboratory and sorted whilst the animals were still alive. Shells less than 1 mm in length were ignored because specimens of this size could rarely be identified with certainty. Specimens larger than this were removed and placed in a labelled sealed tube with a little water. At room temperature the animals died



TABLE 1

Location of the 124 survey sites and distribution of species at the sites. The sites within each catchment are arranged according to geographical location.

Site number		Flow regime	Width in m	<i>Sphaerium lacustre</i> (Müller)	<i>S. corneum</i> (L.)	<i>Pisidium amnicum</i> (Müller)	<i>P. casertanum</i> (Poli)	<i>P. personatum</i> Malm	<i>P. obtusale</i> (Lamarck)	<i>P. milium</i> Held	<i>P. subtruncatum</i> Malm	<i>P. henslowanum</i> (Sheppard)	<i>P. hibernicum</i> Westerlund	<i>P. nitidum</i> Jenyns	<i>P. pulchellum</i> Jenyns	<i>P. tenuilineatum</i> Stelfox
	COLN															
1	SP 034224	P	1				+		+					+		
2	SP 028204	P	2					+						+		
3	SP 027184	P	3											+		
4	SP 057135	P	4		+	+		+						+		
5	SP 073130	P	5		+		+							+		
6	SP 088091	P	5		+									+		
7	SP 103076	P	7		+											
8	SP 142050	P	8		+									+		
9	SP 149032	P	9		+		+			+	+					
10	SP 172992	P	7											+		
SUB	TOTAL				6	1	3	2	1	1	1			8		
	LAMBOURN															
1	SU 328790	I	4				+	+								
2	SU 336779	I	3				+	+								
3	SU 348771	I	2					+								
4	SU 367765	I	4				+	+								
5	SU 384753	P	5				+				+			+		
6	SU 389747	P	7				+			+	+			+		
7	SU 403737	P	7				+			+	+			+		
8	SU 410732	P	10				+				+			+		
9	SU 418723	P	8				+			+	+			+		
10	SU 429707	P	12				+			+	+			+		
11	SU 453693	P	8				+			+	+			+		
12	SU 480681	P	13			+	+	+			+			+		
13	SU 456721	I	3				+	+								
14	SU 454716	I	3				+	+						+		
15	SU 453711	I	3				+	+			+			+		
16	SU 450709	P	4				+			+	+			+		
17	SU 451706	P	4				+			+	+			+		
18	SU 453703	P	4							+	+			+		
19	SU 451698	P	4							+	+			+		
20	SU 452695	P	6								+			+		
SUB	TOTAL					1	16	8		9	14			15		
	FROME															
1	ST 586004	P	2			+	+			+	+			+		
2	ST 537000	P	2								+			+		
3	SY 593976	P	5							+	+			+		
4	SY 624949	P	15			+	+			+	+			+		
5	SY 637947	P	5		+	+				+	+			+		
6	SY 678935	P	3				+				+		+	+		
7	SY 700908	P	5								+			+		
8	SY 772888	I	3					+								
9	SY 769909	P	20			+	+			+	+			+	+	
10	SY 806893	P	30							+	+			+	+	



Site number		Flow regime	Width in m	<i>Sphaerium lacustre</i> (Müller)	<i>S. corneum</i> (L.)	<i>Pisidium amnicum</i> (Müller)	<i>P. casertanum</i> (Poli)	<i>P. personatum</i> Malm	<i>P. obtusale</i> (Lamarck)	<i>P. milium</i> Held	<i>P. subtruncatum</i> Malm	<i>P. henslowianum</i> (Sheppard)	<i>P. hibernicum</i> Westerlund	<i>P. nitidum</i> Jenyns	<i>P. pulchellum</i> Jenyns	<i>P. tenuilineatum</i> Stelfox
FROME <i>continued.</i>																
11	SY 775872	P	4								+					
12	SY 800874	P	5			+	+				+		+	+		
13	SY 811881	P	5				+			+	+		+	+		
14	SY 827868	P	2				+	+		+	+			+		
15	SY 847868	P	2								+			+		
16	SY 868868	P	20				+	+		+	+			+	+	
17	SY 871867	P	1							+	+		+	+		
18	SY 871867	P	10				+			+	+			+		
SUB	TOTAL				1	5	9	3		11	17		4	16	3	
PIDDLE																
1	SY 707994	P	3		+					+	+			+		
2	SY 744953	P	3							+				+		
3	SY 772943	P	5								+			+		
4	SY 830933	P	5			+	+				+			+		
5	SY 835961	P	5				+			+	+			+		
6	SY 877894	P	10			+	+				+	+		+		
7	SY 922877	P	12				+				+			+		
SUB	TOTAL				1	2	4			3	6	1		7		
STOUR																
1	ST 768328	P	1		+		+				+	+		+		
2	ST 776308	P	3		+						+	+		+		
3	ST 813298	P	4			+					+			+		
4	ST 854284	P	2		+		+		+		+			+		
5	ST 791227	P	4		+						+			+		
6	ST 758216	P	4								+					
7	ST 733143	P	3								+					
8	ST 751138	P	4						+		+	+		+		
9	ST 774133	P	2				+			+	+			+		
10	ST 785136	P	15	+	+	+	+				+	+		+		
11	ST 855187	I	1								+			+		
12	ST 824120	P	15		+						+					
13	ST 865084	P	20	+	+		+			+	+	+	+	+		
14	ST 886062	P	30	+			+	+		+	+	+	+	+		
15	SZ 005978	P	2				+	+								
16	SU 014088	P	10				+				+					
17	SZ 012998	P	10				+			+	+		+	+		
18	SZ 048978	P	30							+	+	+		+		
19	SZ 070976	P	30	+			+			+	+	+	+	+		
20	SZ 093960	P	30				+	+		+	+	+		+		
21	SZ 103970	P	30	+			+	+		+	+	+		+		
22	SU 040043	P	2				+	+			+					
23	SU 052024	P	5							+	+			+		
24	SU 063050	P	4								+		+			
25	SU 093076	P	5					+			+		+	+		
26	SU 079022	P	10							+	+			+		
27	SU 097010	P	10		+	+	+			+	+		+	+		
28	SZ 127965	P	8				+	+		+	+	+	+	+		
29	SZ 138936	P	35	+		+	+				+	+		+		
SUB	TOTAL			6	8	4	16	7	2	12	28	12	8	22		



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Site number		Flow regime	Width in m	<i>Sphaerium lacustre</i> (Müller)	<i>S. corneum</i> (L.)	<i>Pisidium amnicum</i> (Müller)	<i>P. casertanum</i> (Poli)	<i>P. personatum</i> Malm	<i>P. obtusale</i> (Lamarck)	<i>P. milium</i> Held	<i>P. subtruncatum</i> Malm	<i>P. henslowanum</i> (Sheppard)	<i>P. hibernicum</i> Westerlund	<i>P. nitidum</i> Jenyns	<i>P. pulchellum</i> Jenyns	<i>P. tenuilineatum</i> Stelfox
	AVON															
1	SU 187378	I	5				+									
2	SU 163596	P	3								+			+		
3	SU 134559	P	4											+		
4	SU 153469	P	8								+			+		
5	SU 137406	P	10			+					+			+		
6	SU 129330	P	8			+	+			+	+	+		+		+
7	SU 072310	P	5		+	+					+	+		+		
8	SU 119306	P	12		+	+	+				+					
9	SU 149292	P	15			+	+	+			+	+				+
10	SU 160277	P	10		+	+	+				+	+		+		
11	SU 108265	P	5				+			+	+			+	+	
12	SU 148134	P	10			+	+				+	+				
13	SU 143053	P	30			+	+				+	+		+		
14	SU 196017	P	3				+				+					
15	SZ 155963	P	20			+	+	+			+	+		+		+
16	SZ 160948	P	2				+			+	+			+		
SUB	TOTAL				3	9	11	2		3	14	7		11	1	3
	TEST															
1	SU 524505	P	6				+									
2	SU 507497	P	10		+		+			+	+			+		
3	SU 487487	P	12				+			+	+			+		
4	SU 461477	P	12		+		+							+		
5	SU 434442	P	20				+				+			+		
6	SU 392404	P	10				+			+	+			+		
7	SU 362369	P	20		+		+				+			+		
8	SU 343317	P	25		+		+			+	+			+		
9	SU 338278	P	20		+		+	+		+	+			+		
10	SU 332264	P	25		+		+			+	+			+	+	
SUB	TOTAL				6		10	1		6	8			9	1	
	ITCHEN															
1	SU 588278	I	2				+	+			+					
2	SU 580296	P	5				+			+	+			+		
3	SU 563317	P	25				+				+			+		
4	SU 523325	P	15		+		+			+	+			+		
5	SU 481282	P	10			+	+			+	+			+		
6	SU 470233	P	25		+		+				+			+		
7	SU 465173	P	10		+	+	+				+			+		
8	SU 447156	P	25		+	+	+			+	+			+	+	
SUB	TOTAL				4	3	8	1		4	8			7	1	
	MEON															
1	SU 685210	I	1				+			+	+			+		
2	SU 652239	I	1				+				+			+		
3	SU 612201	P	5		+		+				+			+		
4	SU 589141	P	7				+			+	+			+		
5	SU 553086	P	5			+	+	+		+	+			+		
6	SU 539045	P	5		+		+	+			+			+		
SUB	TOTAL				2	1	6	2		3	6			6		
TOTAL				6	31	26	83	26	3	52	102	20	12	101	6	3



and rotted within two weeks, so that the empty shells could be washed in ethyl alcohol, dried and stored for later examination.

Samples were collected between 1971 and 1980, generally in the late summer and autumn during periods of stable river flows.

## RESULTS

Thirteen species of Sphaeriidae were recorded from 124 sites (table 1). Four species, *Pisidium casertanum*, *P. milium*, *P. subtruncatum* and *P. nitidum*, were present in all the river systems and a further three species, *Sphaerium corneum*, *P. amnicum* and *P. personatum*, were recorded in all but one. Two species were restricted to a single river system, *S. lacustre* to the Stour and *P. tenuilineatum* to the Avon.

The number of site records show that *P. subtruncatum* and *P. nitidum* were the most common species, being recorded from over 80% of the sites visited. *S. corneum*, *P. casertanum* and *P. milium* were also quite common, occurring at 25% or more of the sites. All other species were recorded at less than 25% of the sites visited, but this group contains *P. amnicum* which was recorded from all but one of the river systems sampled.

Surveys of invertebrates in other river systems (Williams & Hynes 1977, Legier & Talin 1973) have suggested that there is a distinct community associated with sites which have intermittent flow. The sites were therefore classified according to the flow regime, and the percentage occurrence of each species was calculated for both types of site (Fig. 2). Five species were recorded from intermittent sites, with *P. casertanum* and *P. personatum* the most common. These two species were also recorded from a higher percentage of intermittent flow sites than permanent flow sites. This difference was particularly marked in *P. personatum*. All 13 species encountered during the survey were recorded from permanent flow sites and eight occurred only at sites with permanent flow. *P. nitidum* and *P. subtruncatum* were the most abundant at permanent flow sites, but *P. casertanum* and *P. milium* were also frequently recorded.

Both Bishop & Hewitt (1976) and Ellis (1978) suggest that the size of a particular water body has an important influence on the assemblage of species of Sphaeriidae present. The sites were therefore classified according to size, based on channel width, and the distribution of each species among the different categories was calculated (Fig. 3). A correction factor was applied to allow for the different number of sites in each size category. The two species (*P. tenuilineatum* and *P. obtusale*) which were only recorded at three sites were omitted from this calculation.

Four species, *S. lacustre*, *S. corneum*, *P. henslowanum* and *P. hibernicum*, showed the greatest percentage occurrence at sites which were over 25 m in width. *P. pulchellum* was also recorded mostly from larger rivers but showed a maximum at sites 21–25 m in width. *P. amnicum* showed a maximum at smaller sites which were 10–15 m wide. No species was particularly associated with sites less than 10 m wide. The remaining species either showed apparently random fluctuations (*P. personatum*) or were fairly evenly distributed between the site categories (*P. casertanum*, *P. milium*, *P. subtruncatum*, *P. nitidum*).

Chi-square values were calculated (Pielou 1977) to test the association between species. The two species with less than five records were omitted from the calculation. Table 2 presents the Chi-square values for the remaining eleven species and the significant associations are summarized in Fig. 4. This analysis indicated two distinct groups of species. The first consisted of *P. amnicum*, *P. henslowanum*, *S. lacustre* and *P. hibernicum*. As noted earlier, it was these species which showed a preference for the medium or larger-sized sites. The structure of the group was linear and probably represents a transition from *P. amnicum*, which showed maximum occurrence in medium-sized sites, to *P. hibernicum* which was associated



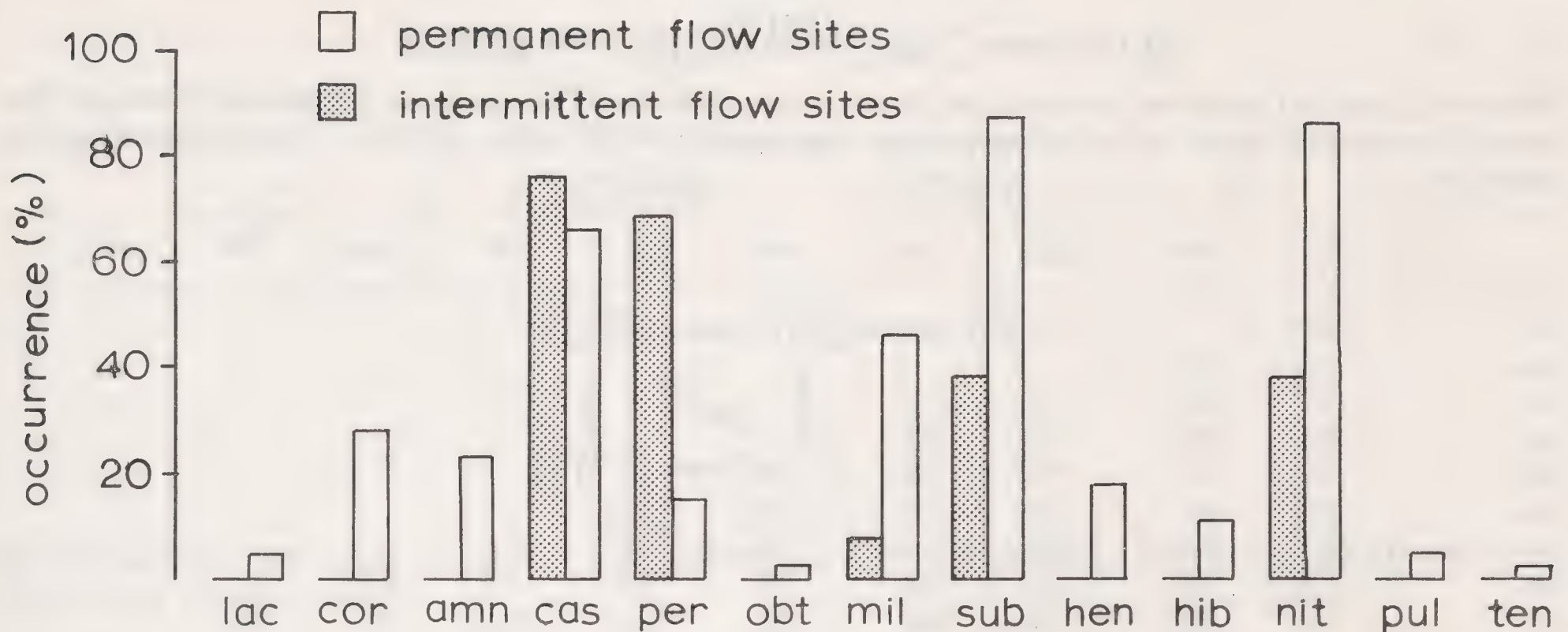


Fig. 2. Percentage occurrence of each species at intermittent and permanent flow sites. The species are designated by the first three letters of the specific name.

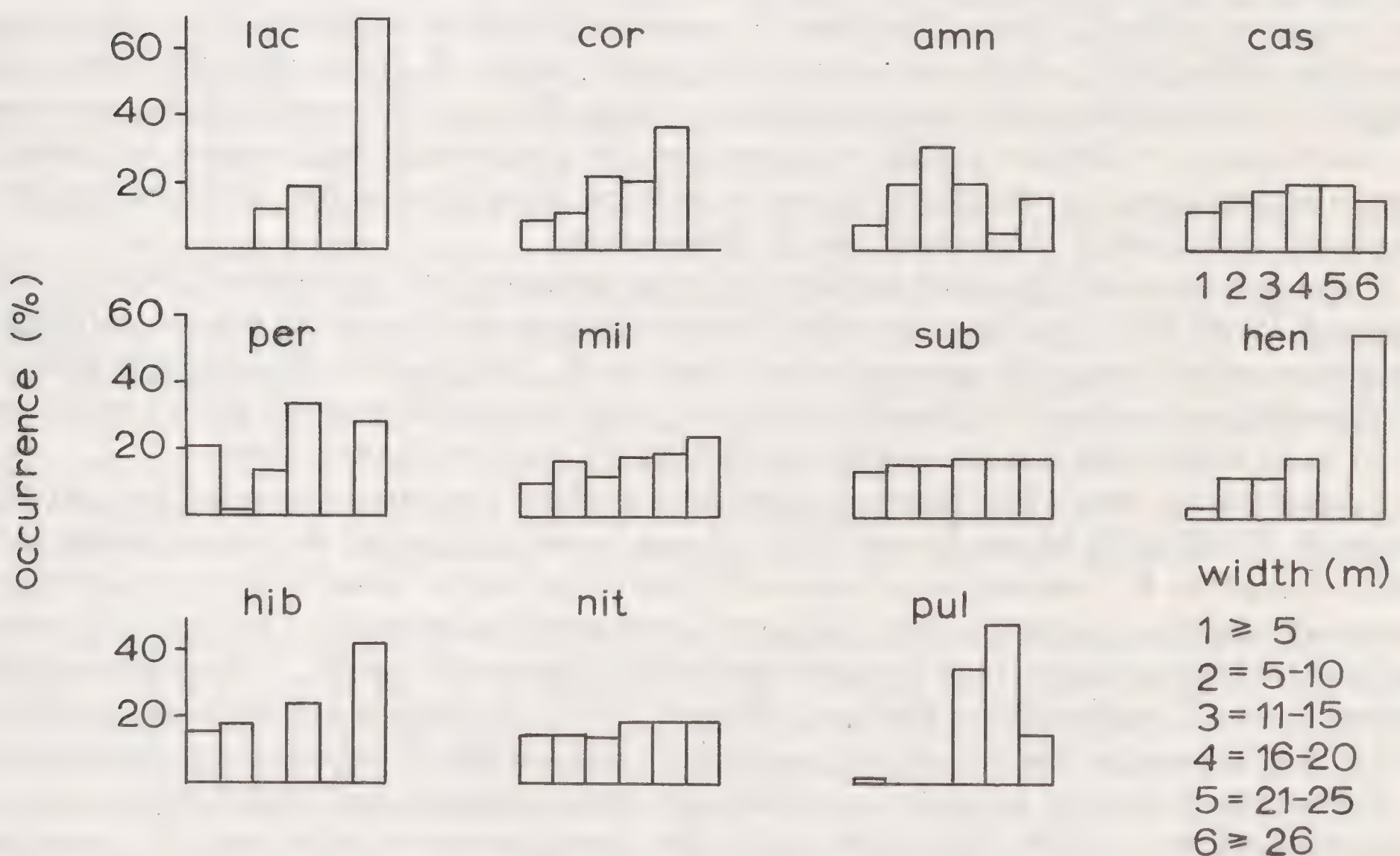


Fig. 3. Percentage distribution of each species at sites classified into six size categories, based on channel width. The species are designated by the first three letters of the specific name.

with the largest size of site. The second species group consisted of *P. subtruncatum*, *P. personatum*, *P. milium*, *P. nitidum* and *P. pulchellum*. There were more between-species associations in this group and it consisted mostly of species that were common and showed no differences in distribution between sites of different size. Two species, *S. corneum* and *P. casertanum* showed no association with any other species.



TABLE 2

Values of  $\chi^2$  obtained in the test of association between pairs of species. The species are designated by the first three letters of the specific name. A pair of species are associated ( $p > 0.95$ ) when  $\chi^2 > 3.84$ . Positive associations are underlined.

	lac	cor	amn	cas	per	mil	sub	hen	hib	nit
cor	0.0									
amn	0.6	0.4								
cas	1.7	0.1	2.1							
per	0.1	3.8	1.1	2.1						
mil	0.7	1.7	2.3	3.3	2.3					
sub	0.4	0.4	1.5	2.6	<u>11.6</u>	<u>13.5</u>				
hen	<u>26.6</u>	0.1	<u>10.1</u>	1.2	0.6	0.2	3.8			
hib	<u>7.4</u>	2.9	0.6	0.1	0.0	2.3	1.7	1.7		
nit	0.4	0.3	0.6	0.0	<u>10.4</u>	<u>14.5</u>	<u>10.7</u>	0.6	0.3	
pul	2.4	0.9	0.1	0.2	0.6	<u>6.4</u>	0.4	2.8	2.3	0.4

## DISCUSSION

During the present survey, *S. lacustre* was only recorded from six sites in the middle and lower reaches of the R. Stour. This may be associated with its preference for habitats with slow flow (Ellis 1978), which occur more frequently in the R. Stour than the other rivers sampled. *S. lacustre* showed its maximum occurrence at sites over 25 m wide which agrees with the observations by Boycott (1936) who describes the species as being common in rivers. He also comments that it is often found alone or with few other species, but in this survey it was associated with both *P. hibernicum* and *P. henslowanum*.

*S. corneum*, described by other workers as being common and widespread (Boycott 1936, Kuiper & Wolff 1970), has been recorded from all the river systems in the survey. Although it was not recorded during the present survey from the R. Lambourn it does occur in this river (McDonald pers. comm.). It showed a tendency to occur more frequently at sites which were 21–25 m in width and was recorded only from sites with permanent flow.

*P. amnicum* has previously been reported from lowland streams and rivers (Boycott 1936, Kuiper & Wolff 1970, Meier-Brook 1975). It was recorded from all the river systems in the survey except the R. Test and occurred at all types of site except those with intermittent flow. *P. amnicum* was found slightly more frequently in streams that were 10–15 m wide. In eastern England this species appears to be associated with *P. supinum* Schmidt, *P. henslowanum* and to a lesser extent *P. subtruncatum* (Bishop & Hewitt 1976). *P. amnicum* did show an association with *P. henslowanum* in this survey but not with *P. subtruncatum*. *P. supinum* was not recorded.

*P. casertanum* is often regarded as being the most common and widespread species of Sphaeriidae (Boycott 1936, Ellis 1978) and in this survey it was recorded from all types of site. *P. casertanum* occurred in all the river systems, in sites with either permanent or intermittent flow and showed no difference in distribution at sites of different size. Bishop & Hewitt (1976) observed that it was associated with both *P. supinum* and *P. subtruncatum*, but in this survey it was not associated with any other species. *P. casertanum* and *P. personatum* were frequently recorded from sites with intermittent flow and in experimental studies (Hinz 1972, Danneel & Hinz 1974) both *P. casertanum* and *P. personatum* were found to have resistance to dessication, with the former the more resistant of the two.

*P. personatum* has previously been recorded from a variety of habitats by Boycott (1936) and Kuiper & Wolff (1970). They describe the species as being characteristic of small temporary stagnant waters, which are generally unsuitable for other molluscan species.



AMN=HEN=LAC=HIB

COR

CAS

SUB=MIL=PUL

$$\begin{array}{ccc} \parallel & \diagdown & \parallel \\ \text{PER} & = & \text{NIT} \end{array}$$

Fig. 4. Diagrammatic representation of between-species associations. The species are designated by the first three letters of the specific name.

However, Meier-Brook (1975) reports that in flowing waters this species is characteristic of streams fed by ground water. In this survey the species was particularly characteristic of sites with intermittent flow which are small and temporary in nature, but receive a high proportion of their discharge from ground water. Both Boycott (1936) and Bishop & Hewitt (1976) state that this species is not associated with other molluscan species and often occurs alone. In this survey it was associated with both *P. subtruncatum* and *P. nitidum*.

One of the less frequently recorded species during the survey was *P. obtusale*. Boycott (1936) and Kuiper & Wolff (1970) describe the typical habitat for the species as being similar to that of *P. personatum*. A preference for shallow ponds has also been suggested (Mitropolskii 1969). It was recorded from only three sites, two on the R. Stour and one on the R. Coln. At all three sites the river was slow flowing and less than 5 m wide.

Another species which has been described as being widely distributed is *P. milium* (Boycott 1936, Ellis 1978). This was confirmed in the present survey, as it was recorded from all types of site. *P. milium* showed an association with *P. nitidum*, *P. subtruncatum* and *P. pulchellum*, although Bishop & Hewitt (1976) found no association with other species.

*P. subtruncatum* and *P. nitidum* were the two most common species in the survey being recorded from all types of site throughout the river systems. The two species show a preference for lowland rivers (Boycott 1936, Meier-Brook 1975) and in this survey were closely associated with each other, as shown by Bishop & Hewitt (1976). Both species were also associated with *P. milium* and *P. personatum*, but this was not observed by Bishop & Hewitt (1976).

*P. henslowanum* was generally restricted to the lower sites on the R. Stour and R. Avon with a single record at one of the lower sites on the R. Piddle. This gave rise to its maximum occurrence at sites which were greater than 25 m wide. Although this species is widespread in southern England (Kerney 1976), it was surprisingly absent from the other river systems. An earlier record from the tidal limit of the R. Frome (Kerney pers. comm.) was not confirmed during the present survey. Both Boycott (1936) and Bishop & Hewitt (1976) state that *P. henslowanum* is associated with *P. amnicum* and this was also observed in the present study. *P. henslowanum* was also associated with *S. lacustre*. However, no significant association was apparent with *P. nitidum*, *P. subtruncatum* or *P. casertanum*, differing from the results of Bishop & Hewitt (1976).

Although *P. hibernicum* is not common in the south of England (Boycott 1936, Kerney 1976), it was recorded from 8 sites on the Stour and 4 sites on the Frome system. It did not conform to the pattern described by Ellis (1978) of being found particularly in smaller streams, but showed a tendency to occur at sites greater than 25 m wide. However, it was recorded from most site size categories, which is consistent with the description by Meier-Brook (1975) of it occurring in both rivers and streams.



*P. pulchellum* appears to have a scattered distribution in Britain (Kerney 1976) and was not commonly encountered during the survey. It was recorded from the Avon, Frome, Test and Itchen and its preference for 'fine sediments with clean water' (Boycott 1936) may explain its limited distribution in the survey and throughout the British Isles.

The final species, *P. tenuilineatum*, has a very restricted distribution in Britain (Kerney 1976) and in this survey was recorded from only three sites on the R. Avon.

During this survey the sites were similar in many chemical and physical characteristics and the only environmental variables considered were constancy of flow and channel width. It is possible that size of river may only be representative of some other factor, e.g. substratum composition, which is influencing the distribution of species. The results in the present study are generally in agreement with the habitat preferences given by Boycott (1936), Kuiper & Wolff (1970) and Meier-Brook (1975), although, as noted above, there were several discrepancies. However the description of habitat preferences by these authors is generalized, such that a single category given by these authors, includes a range of sites in the present survey.

Two of the associations between species as demonstrated by Bishop & Hewitt (1976) were also observed during this survey. However 4 other associations described by them were not observed and 4 new associations were recorded. Bishop & Hewitt (1976) speculate on the factors which are influencing the distribution of Sphaeriidae and the results presented here neither invalidate nor confirm their ideas. In conclusion it is apparent that much remains to be discovered about the factors controlling the distribution of Sphaeriidae.

#### ACKNOWLEDGEMENTS

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# LATE PLEISTOCENE LAND MOLLUSCA IN THE CHANNEL ISLANDS

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(Accepted for publication 18 October 1981)

*Abstract:* Pleistocene land Mollusca from five sites in Guernsey and Jersey are listed. They reflect very cold conditions, and the faunas resemble those from similar deposits in Normandy and Brittany. Ages in the Devensian (last) glacial stage are suggested. The first record of *Columella columella* (Martens) for the Channel Islands is noted.

## INTRODUCTION

The number of non-marine molluscan species living in the Channel Islands is rather small, with only the freshwater and dune habitats providing any abundance of specimens (Tomlin and Marquand 1903, Chatfield 1975, Kerney 1976). Pleistocene Mollusca are even less well known, and their preservation is made very difficult by the general absence of calcareous rocks. However, land Mollusca of Peistocene age are known from both the major islands of the group, and examination of their occurrence during the recent geological survey of the islands, together with reconsideration of material in the museum of La Société Jersiaise, has allowed them to be described.

In all cases the preservation of the Mollusca is due to the calcium carbonate content of loess (windblown dust) or of head (solifluxion debris) derived from it. Although the amounts of calcium carbonate in the loess are low, these deposits are sufficiently calcareous to preserve shells from leaching in favourable circumstances. This is especially so where calcareous concretions (Lössmanchen) occur. In these cases, Mollusca are preserved both in the concretions and in the surrounding matrix.

Bulk samples of loess or loessic head were collected from two localities, and concretions from a third site. The Mollusca were separated from the loess by passing the sediment through sieves down to 0.5 mm aperture (30 mesh). Separation of the shells from the concretions was however impossible. All attempts, whether physical or chemical, resulted in destruction of the Mollusca before the breakdown of the matrix.

## MOLLUSCAN LOCALITIES AND SPECIES

### *Guernsey*

The only site which has yielded land Mollusca in Guernsey is St Martin's Point (WV344748), where they are preserved both in calcareous loessic head and lössmanchen. The deposit is a thin loess which has been banked against a cliff of gneiss. Contemporary solifluxion or later slumping has incorporated granules and larger angular fragments of quartz and feldspar from the weathered solid rock into the loess to form a fine-grained head.

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A 30 kg sample was taken from the richest molluscan layer, exposed at the base of the present-day vegetated slope; this yielded 1432 individuals of five species:

<i>Oxyloma pfeifferi</i> (Rossmässler)	106
<i>Columella columella</i> (Martens)	11
<i>Pupilla muscorum</i> (L.)	571
<i>Vitrina pellucida</i> (Müller)	1
<i>Trichia hispida</i> (L.)	743

Other records from this site (Girard 1966) include *Helix aspersa* Müller, *Candidula intersecta* (Poiret), *Cernuella virgata* (da Costa), *Lauria cylindracea* (da Costa), *Vertigo pygmaea* (Draparnaud), *Cochlicopa lubrica* (Müller) and *Clausilia bidentata* (Ström). This list is ecologically incompatible with such species as *Columella columella* and *Oxyloma pfeifferi* noted above and is almost certainly not from the loess but from the modern soil on this steep slope. In the sample sieved in the current investigation, one specimen of *C. lubrica* was recovered, but its condition was unlike that of the genuine Pleistocene species and was also probably modern.

As is usual with Pleistocene slope deposits many of the shells were broken, but enough intact examples of *Pupilla muscorum* were obtained to show that the form present at St Martin's Point was rather larger and more cylindrical than modern British specimens and resembles the late-glacial form described by Kerney from Kent (Kerney *et al.* 1963). The specimens of *Oxyloma pfeifferi* are of the small fossil form usually referred to as *O. pfeifferi schumacheri* Andreae by British authors (e.g. Sparks *in* Shotton 1968).

### Jersey

Land Mollusca are known from four sites in Jersey. Three of these were noted by Kennard (*in* Mourant 1935) – St Aubin (c. WV607483), La Motte (WV674460) and Portelet (c. WV601472) – while the site at Belval (WV709527) was found during the geological survey of the island in 1974. New samples of loess and concretions were collected from La Motte and Belval. The sites at St Aubin and Portelet are not now visible, so the Mollusca described by Kennard and lodged in the Société Jersiaise museum in St Helier have been re-examined, together with Kennard's material from La Motte.

*St Aubin.* The exact locality of collection here is uncertain. Much of the cliff section south of St Aubin's harbour is in loessic head but no Mollusca or concretions have been found since the 1930's. The loess now visible in the upper parts of the sections is highly decalcified making the preservation of Mollusca unlikely. The specimens from the Société Jersiaise museum labelled 'St Aubin' (SJM c 13892) are in two concretions and consist of one specimen of *Pupilla muscorum* and two indeterminate succineids (recorded by Kennard as '*Succinea arenaria*'). As at St Martin's Point the *P. muscorum* is a rather large and cylindrical example.

*Portelet.* This site is also now lost. The bay is backed by cliffs of loessic head which is still calcareous in patches, but no concretions or Mollusca could be found during mapping in 1974. Material from Portelet in the Société Jersiaise museum (SJM c 1388) consists of a single concretion with two indeterminate succineids and an external cast of *Trichia hispida*, identified by Kennard as '*Succinea arenaria*' and '*Trochulus hispidus*' respectively. Kennard (*in* Mourant 1935) also recorded *Pupilla muscorum* but his specimens have not come to light.

*La Motte.* Among the Mollusca in the Société Jersiaise museum identified by Kennard is one example of *Pupilla muscorum* from La Motte (SJM c 1393). Although the label states that the specimen is from a loess concretion, very little matrix adheres to the shell so it probably came from non-concretionary loess.

Unlike the preceding two sites the mollusc-bearing horizon at La Motte is still visible. The main concentration is on the north-east corner of the islet in the bottom 0.7 m of the loess.



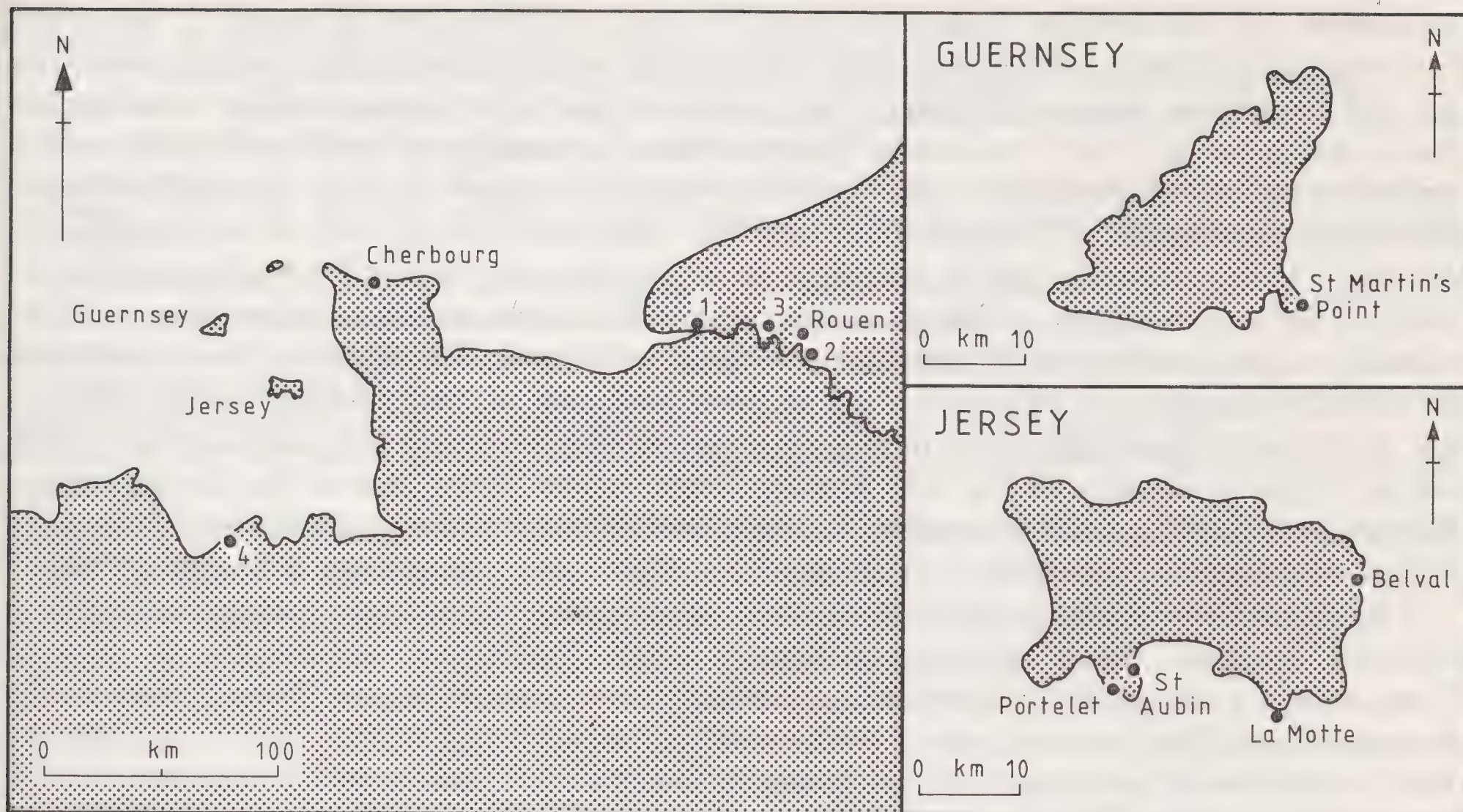


Fig. 1. The location of Late Pleistocene molluscan localities in the Channel Islands and on the adjacent coast of France. 1, Tancarville; 2, Mesnil-Esnard; 3, Roumare; 4, Port Morvan.

The deposit here is a true stoneless loess, fully decalcified in its topmost layers but still calcareous up to 1 m from the diorite bedrock. Small quantities of non-fossiliferous concretions occur at the northeasternmost corner of the island and for about 20 m to the north-west. Around these, the loess is at its most calcareous. A 5 kg sample yielded the following species:

cf. *Oxyloma* sp. 6 (juveniles only), *Pupilla muscorum* (L.) 9, *Vallonia costata* (Müller) 1, *Trichia hispida* (L.) 1.

As at the other sites, the specimens of *P. muscorum* were larger than those from either modern dune habitats in Jersey or from Britain.

*Belval*. The loessic head here contains large tabular concretions in its uppermost metre. These are sparsely fossiliferous and examination of about 5 kg of concretions yielded seven poorly preserved succineids. The identity of these is uncertain. One was examined by Dr. M. P. Kerney, who reported that it was not an *Oxyloma*, but most probably *Succinea oblonga* Draparnaud.

#### OTHER SIMILAR FAUNAS

Faunas dominated by *Pupilla muscorum* and *Trichia hispida* are recorded from loess and loessic head on the French mainland near the islands. In Normandy, Lautridou and Puissegur (1977) note faunas consisting largely of these two species (together with *Succinea oblonga*) from three sites in Seine Maritime (Tancarville, Mesnil-Esnard and Roumare). At the first site the shells are contained within loessic head, at the latter two in calcareous loess. In Brittany, Monnier (1974) records a fauna dominated by *P. muscorum* (23% of the total) and *T. hispida* (65.5% of the total) from calcareous, sandy loess at Port Morvan (Cotes du Nord). At all four of these sites the faunas are held to indicate cold, or at least highly continental



conditions. At Tancarville, Lautridou and Puissegur differentiate an upper *P. muscorum*/*T. hispida* fauna from a stratigraphically inferior one which contains also *Arianta arbustorum* (L.) and *Bradybaena fruticum* (Müller). They consider this earlier fauna to reflect a cool rather than a cold climate. The *P. muscorum*/*T. hispida* fauna is thought to typify very cold, stadial conditions in the Weichselian (last) glacial, while the more diverse *Arianta*/*Bradybaena* assemblage is thought to represent the warmer conditions at the end of an interglacial. Monnier (1974) supports this in Brittany, as he regards the *Pupilla*/*Trichia* fauna there as evidence for a cold climate of full glacial intensity. The same conditions of extreme cold are probably represented by the Mollusca in the Channel Islands. In particular, the occurrence of *Columella columella* at St Martin's Point suggests a climate of some severity as this species is now restricted to mountain areas in Scandinavia and the Alps (Kerney and Cameron 1979) and is a typical member of the cold climate faunas of the latter part of the last glaciation (Kerney *et al.* 1963). A cold climate is also suggested by the occurrence of the small fossil form of *Oxyloma pfeifferi* ('*schumacheri*') at St Martin's Point (see also Sparks *in* Shotton 1968).

The association of *Pupilla muscorum* and succineids is well known at a range of localities in southern England where sediments formed under periglacial conditions. At present *P. muscorum* is a xerophile; by contrast succineids favour marshy places. Their occurrence in the same deposit has been explained as due either to the mixing of shells from two habitats by slope or sheet-wash processes, or to a change of tolerance of *P. muscorum* allowing it to live in damper habitats than it now occupies (Kerney *et al.* 1963). Either of these hypotheses would explain this association in the Channel Islands. There is however no direct evidence from the Mollusca for the dry conditions suggested by Lautridou and Puissegur (1977) for the accumulation of the loess. It is possible that the climate was a predominantly dry one, but that the local environment provided the damper habitats needed by the succineids due to the impeded drainage and low evaporation rates typical of periglacial conditions (Kerney 1971).

#### AGE OF THE FAUNA

There is no evidence from the fauna itself to suggest any particular age in the Late Pleistocene. The *Pupilla*/*Trichia* assemblages of Normandy are thought by Lautridou (1977) to occur in both Upper and Lower Pleniglacial (=Weichselian/Devensian) deposits, while Monnier (1974) regards the deposits which contain this fauna in Brittany as being of late Saalian age.

The loess and head containing the Mollusca in the Channel Islands always overlie the low ('8 m') raised beach of the area. This probably places these deposits in the Weichselian (Devensian) glacial stage (Keen 1978). It is impossible to be more precise about their age.

#### ACKNOWLEDGEMENTS

I am grateful to B. W. Sparks for confirming the identification of the Mollusca from St Martin's Point, to A. E. Maurant F.R.S. for sampling the concretions from Belval, and to G. Drew, curator of La Société Jersiaise museum, for access to the collections. This paper was read in draft by Dr. M. P. Kerney and I am especially grateful for his comments.

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## REVIEW

*Intertidal Invertebrates of California*. By R. H. Morris, D. P. Abbott and E. C. Haderlie. Stanford University Press, 1980. 690 pp., 200 colour plates. \$30.00. ISBN 0 8047 1045 7

Some of the most innovative work in intertidal ecology over the last 20 years or so has emanated from the laboratories and universities of the north-west coast of America. To most of us in Europe, the fauna is unfamiliar and the names referred to in books and papers mean little without some association with illustrations or specimens. Although molluscs are generally well served by identification guides, other phyla are not so well covered and this book is thus a welcome arrival.

This very large book is a systematic catalogue of the common invertebrate animals of the Californian coast. It measures 28×22 cm, weighs 2.8 kg and has 200 pages of colour photographs and 690 pages of text. It follows a systematic treatment from protozoa to insects and each of the 28 chapters concerning animal groups is written by D. P. Abbott and E. C. Haderlie in combination with 31 co-authors and specialists in the groups concerned. Each chapter has a general introduction on the major features, relationships and biology of the animal groups concerned and is followed by an account of each species. The colour plates are in a separate part of the book, so the thumb-nail sketch with each species provides a welcome reminder. There is a brief description of each animal followed by a summary of what is known of its biology and ecology with a list of key references. The book is an absolute mine of information and widely dispersed works concerning feeding habits, reproductive biology, physiology, distribution etc. have been collected together in succinct summaries. Over 5500 references have been cited and in all 288 species of molluscs have been considered.

The core of the book is the colour plates, which were largely taken by R. H. Morris and are on the whole very good with most of the animals being photographed live or freshly collected. For the molluscs there are about 300 individual photographs: the 70 or so pictures of opisthobranchs are striking but the prosobranchs are not consistently orientated and for many the apertures are not shown.

The book is not just relevant to California, for as similar or related species occur in many other parts of the world the book is a treasure trove of information to anyone interested in the biology of intertidal animals. If used in conjunction with the excellent ecological summary 'Pacific Seashores' by Thomas Carefoot (University of Washington Press) the two books provide a superb guide to the animals and their ecology on this rich and varied coastline. Finally, the book is very well produced and very good value for money, in fact a bargain.

JOHN TAYLOR



# VICE-COMITAL CENSUS OF THE NON-MARINE MOLLUSCA OF THE BRITISH ISLES (8th EDITION)

M. P. KERNEY\*

(Accepted for publication 30 May 1981 – Revised to 23 October 1981)

*Abstract:* The distribution of the non-marine Mollusca of the British Isles is shown by listing the botanical vice-counties from which there exist properly authenticated records, a system begun by the Conchological Society in 1876. Though this is a relatively coarse way of plotting geographical data, the ‘census’ system remains useful as a framework for assessing the reliability of information received during grid mapping and other detailed surveys. The last edition was published in 1951.

## INTRODUCTION

The last (7th) edition of the vice-comital Census of British and Irish non-marine Mollusca was published thirty years ago (Ellis 1951, Kerney 1966). Boycott (in Roebuck 1921) and Ellis (1951) describe the long history of the idea. In 1961 grid mapping using 10 kilometre squares began, culminating fifteen years later in a national atlas showing distributions in a much more detailed way than was possible under the old system (Kerney 1976).

The vice-comital method has nevertheless retained a residual usefulness. Its essence is that no record shall be included unless it has been verified from actual specimens submitted to the Society’s referees, and the particulars entered up under the appropriate vice-county in the Census volumes held up by the Society. A sound framework is thus created against which the reliability of the very much larger number of field records accumulated during grid mapping—often by relatively inexperienced workers and unsupported by voucher specimens—can be assessed. With the exception of some common segregates, increments continue to be published annually in the *Non-marine Recorder’s Report* in the *Journal*.

It therefore seems worthwhile publishing this simple summary, without maps or tables. The exact boundaries of the 112 British vice-counties (which often differ significantly from the modern counties) can be determined from the maps at a scale of 1:625,000 published by the Ray Society (Dandy 1969). The 40 Irish vice-counties are identical with the present counties, subdivided in some cases as indicated by Ellis (1951). A transparent overlay allowing easy correlation between vice-counties and the dots of the *Atlas* maps is included in the set published by the Biological Records Centre (Anon 1978). The numbering of the Irish vice-counties follows the Praeger system (H1 to H40, Praeger 1896), now universally adopted; the correlation of this with the old Conchological Society Roebuck system (113 to 148) used in earlier Censuses is given overleaf.

It must be remembered that these data are cumulative, having been collected over a period of more than a century, and therefore offer no guarantee that species continue to exist within particular divisions; some indeed are certainly extinct. A few ‘verified’ records given in earlier editions have been deleted, for a variety of reasons. Unverified records (marked in *italic* type in the 1921 and 1951 editions) and those based on fossils have been excluded,

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though many are used on the *Atlas* maps. Adventives, greenhouse aliens, short-lived introductions and the like are also not considered here. Conversely, a few vice-comital records do not appear at all in the *Atlas* owing to lack of sufficiently precise locality data (e.g. *Pupilla muscorum*, 'near the sea, Elginshire' (v.c. 95), G. Gordon leg., J. W. Taylor det. before 1890).

Nomenclature and taxonomic order are as in the 1976 *Atlas*. Some additional species (*Ferrissia wautieri* (Mirolli), *Vertigo genesii* (Gredler), *Arion lusitanicus* Mabilie seg., *A. 'lusitanicus'* Quick, *A. hortensis* Férussac seg., *A. distinctus* Mabilie, *Limax flavus* L. seg., *Euconulus fulvus* (Müller) seg., *E. alderi* (Gray)) have been inserted in their appropriate places.

The Census is to a very large extent the work of my predecessors as non-marine Recorders of this Society. I should like particularly to thank Mr. A. E. Ellis, who first aroused my interest in distribution studies, and the late A. W. Stelfox, who taught me about *Pisidium* and a great deal concerning the Mollusca of Ireland.

Kerry South	148S	H1	Dublin	124	H21
Kerry North	148N	H2	Meath	123	H22
Cork West	147	H3	Westmeath	132	H23
Cork Mid	146M	H4	Longford	133	H24
Cork East	146E	H5	Roscommon	134	H25
Waterford	145	H6	Mayo East	137	H26
Tipperary South	144	H7	Mayo West	138	H27
Limerick	142	H8	Sligo	136	H28
Clare	141	H9	Leitrim	135	H29
Tipperary North	143	H10	Cavan	121	H30
Kilkenny	129	H11	Louth	122	H31
Wexford	127	H12	Monaghan	117	H32
Carlow	128	H13	Fermanagh	120	H33
Leix (Queen's Co.)	130	H14	Donegal East	119E	H34
Galway South-East	140S	H15	Donegal West	119W	H35
Galway West	139	H16	Tyrone	118	H36
Galway North-East	140N	H17	Armagh	116	H37
Offaly (King's Co.)	131	H18	Down	115	H38
Kildare	125	H19	Antrim	114	H39
Wicklow	126	H20	Derry	113	H40

Note also that the Channel Islands, here numbered 0, in conformity with Ellis (1951), are now more usually labelled 113.

#### VICE-COMITAL DISTRIBUTIONS

\*=species not in Ellis (1951).

**Theodoxus fluviatilis.** 5–9, 11, 13–41, 53–65, 111; H5–19, H21–29.

**Viviparus viviparus.** 3, 6–8, 12, 13, 15–25, 27–42, 47, 50, 53–59, 61–64.

**Viviparus contectus** (= *fasciatus* in Ellis). 11, 17, 19–34, 53–56, 58, 59, 61–64.

**Valvata cristata.** 3, 5–39, 41–43, 45, 49, 50, 52–67, 69, 70, 72, 73, 75–77, 79–88, 90, 95, 99, 105, 106, 111; H1–33, H35–40.

**Valvata macrostoma.** 11, 14, 23, 26–29, 53.

**Valvata piscinalis.** 1, 3–43, 45, 47–90, 92, 96, 98, 99, 101, 103, 108–110; H1–40.

**Pomatias elegans.** 1–17, 19–30, 32–38, 41, 44, 45, 49–51, 53, 54, 60, 62, 64, 69; H9.



- Hydrobia ventrosa** agg. 0, 5, 6, 9–11, 13–16, 18, 19, 25, 27, 28, 41, 50, 52–54, 61, 66, 75, 82, 98, 110–112; H9, H12, H16, H17, H38, H39.
- \*Hydrobia ventrosa** seg. 0, 13–15, 18, 19, 25, 28, 53, 61, 82, 110, 112.
- \*Hydrobia neglecta**. 0, 25, 27, 28, 53, 75, 98, 110, 111; H9.
- Hydrobia ulvae**. 0–6, 9–11, 13–16, 18, 19, 25, 27, 28, 35, 41, 44–46, 48–54, 58–62, 66–70, 72–75, 82–85, 90, 92, 96, 98–101, 103–108, 110–112; H1–6, H8, H9, H12, H15–17, H20–22, H27, H28, H31, H34–36, H38–40.
- Pseudamnicola confusa**. 13, 16, 25, 27, 28, 34, 54; H6, H8, H9, H11–13. Many extinctions.
- Potamopyrgus jenkinsi**. 0–98, 101–105, 108–112; H1–31, H33–40.
- Marstoniopsis scholtzi**. 25, 28, 58, 59.
- Bithynia tentaculata**. 1, 3–43, 47, 50, 53–70, 72–78, 80, 82–84, 86, 95, 99, 100, 102; H2–34, H36–40.
- Bithynia leachii**. 5–8, 11, 12, 14–34, 36–40, 47, 50, 53–58, 61–65, 86; H10–15, H18, H19, H21–24.
- Assimineia grayana**. 15, 16, 18, 19, 25, 27, 28, 53, 54, 61.
- Acicula fusca**. 1–6, 8–18, 20, 22–25, 30, 32–38, 41–45, 48–52, 56, 60, 62–71, 73–76, 83, 98, 100, 102–105; H1–31, H33–40.
- Carychium minimum** seg. 0–70, 72–111; H1–29, H33–40.
- Carychium tridentatum**. 0–111; H1–29, H31, H33–40.
- Ovatella myosotis**. 0–6, 9–11, 13–16, 18, 19, 25, 27, 28, 34, 35, 41, 44, 45, 48–54, 58–62, 66, 69–73, 82, 83, 96, 98, 103, 106, 107; H1–3, H5, H6, H8, H9, H11, H12, H15–17, H21, H22, H27, H28, H31, H34, H38–40.
- Leucophytia bidentata**. 0, 1, 3–5, 9, 10, 13, 16, 18, 19, 25, 34, 41, 45, 71, 82, 98, 100, 101, 112; H5, H6, H9, H15–17, H21, H22, H31, H35, H38, H40.
- Aplexa hypnorum**. 0, 1, 3–42, 45, 47–67, 69–71, 75, 81–83, 86–89, 99, 103, 109, 110; H1, H2, H4–36, H38–40.
- Physa fontinalis**. 3–45, 47–90, 92, 95, 96, 98–100; H1–40.
- Physa** spp., not *fontinalis* (excluding greenhouse occurrences). 0, 1, 3, 6–11, 16–18, 20–22, 24–26, 30–34, 38–41, 53, 55, 56, 58, 59, 62–64, 66. Species records (*acuta*, *heterostroph*a etc.) are mostly unreliable owing to the confused taxonomy of this genus.
- Lymnaea truncatula**. 0–112; H1–40.
- Lymnaea glabra**. 0–2, 9, 11, 13, 14, 16, 18–20, 22, 25, 28, 37, 39, 40, 45, 47, 48, 53, 54, 58, 59, 61–67, 69, 70, 77, 81, 83, 86, 87, 89; H12. Many extinctions.
- Lymnaea palustris**. 0–80, 82–90, 92, 93, 95, 96, 98–101, 106, 109, 110; H1–40.
- Lymnaea stagnalis**. 0, 1, 4–43, 47, 50, 52–70, 72, 77, 79, 80, 82–85, 98; H5–19, H21–34, H36–40.
- Lymnaea auricularia**. 3–8, 10–45, 47–50, 52–64, 66–70, 72, 73, 76, 77, 80–83, 85, 87, 88, 94–96, 99; H4–16, H18, H19, H21–24, H26–31, H33, H35–39.
- Lymnaea peregra**. 0–112; H1–40.
- Myxas glutinosa**. 15, 17, 22–25, 27, 33, 34, 38, 48, 54, 61, 62, 69; H9, H14, H15, H17–19, H21–25, H28, H34, H37–39. Many extinctions.
- Planorbis planorbis**. 3–9, 11–42, 44, 47, 52–67, 69, 70, 72, 73, 76, 77, 79, 80, 82, 83, 85; H2, H4–26, H28–33, H35–40.
- Planorbis carinatus**. 3, 5–42, 47, 50, 51, 53–70, 73, 75–77, 82, 83, 85, 89, 98–100; H4, H5, H7–15, H17–19, H21–40.
- Anisus leucostoma**. 0–78, 80–87, 89, 90, 93, 95, 96, 99, 100, 102–104, 106–111; H1–40.
- Anisus vortex**. 0, 3, 5–42, 47, 50–65, 69, 70, 73, 78, 82, 83, 85, 86, 90; H9, H15, H17–19, H22–25, H28–31, H33, H38.
- Anisus vorticulus**. 13, 14, 21, 25, 27.



- Bathyomphalus contortus.** 2-43, 46-83, 85-96, 98-102, 104-106, 109, 111, 112; H1-19, H21-40.
- Gyraulus laevis.** 2, 3, 6, 9, 13, 15, 17, 18, 21, 23-25, 27, 28, 30-32, 35, 37-43, 45, 48, 49, 52, 53, 55-57, 59, 61-70, 72, 75-78, 80-83, 85-87, 90, 92, 93, 95, 96, 98-100, 103, 108-112; H1, H3, H5-7, H9-11, H15, H16, H20, H21, H23, H27-29, H31, H35, H37-39.
- Gyraulus acronicus.** 22-24.
- Gyraulus albus.** 1-96, 98-101, 103, 104, 106, 107; H1-40.
- Armiger crista.** 0-42, 45-85, 87-90, 92-96, 98-101, 103-112; H1, H2, H4-40.
- Hippeutis complanatus.** 1-45, 47, 49-70, 72-77, 79-88, 90, 92, 93, 95, 106; H1-24, H26-33, H35-39.
- Segmentina nitida.** 0, 11, 12, 14-18, 20-23, 25-29, 31, 32, 37, 47, 53, 54, 56, 59-61, 63, 64. Many extinctions.
- Planorbarius corneus.** 3, 6-42, 47, 50, 53-67, 69, 71, 72, 77, 82, 83, 93, 99; H7, H8, H14, H19, H21-24, H36-40.
- Menetus dilatatus.** 21, 48, 58, 59, 63.
- Ancylus fluviatilis.** 0-111; H1-40.
- \*Ferrissia wautieri.** 10, 11, 14, 28, 30, 63.
- Acroloxus lacustris.** 3, 6-43, 45, 47, 48, 51-67, 69, 70, 72-75, 77, 79-90, 92, 93, 109; H2, H5, H7-15, H17-19, H21-26, H28-34, H37-39.
- Catinella arenaria.** Dissection records only. 4, 69; H10, H14, H18, H27.
- Succinea oblonga.** Dissection records only. 14, 15, 64, 69, 75, 82, 84, 86-88; H1-6, H8, H19, H22, H29, H33, H34, H39.
- Succinea putris.** 0, 2-58, 61-70, 72, 73, 79 (other Scottish records not verified by dissection); H1-33, H37-40.
- Oxyloma pfeifferi.** 0-112; H1-40.
- Oxyloma sarsi** (= *elegans* in Ellis). Dissection records only. 19, 20, 25, 27.
- Azeca goodalli.** 1, 4, 6-8, 11-17, 19, 20, 22-27, 29, 30, 32-43, 47, 48, 50, 53-70, 87.
- Cochlicopa lubrica.** 0-112; H1-40.
- Cochlicopa lubricella** (= *minima* in Ellis). 0-112; H1-29, H31, H33-40.
- Pyramidula rupestris.** 0-3, 5-11, 13-17, 20, 22-24, 30, 32-39, 41, 42, 44-46, 48-53, 55, 57, 59, 60, 62-66, 69-71, 77, 83, 88, 89, 98, 104, 108; H1-19, H21-36, H39.
- Columella edentula** agg. 0-112; H1-40.
- \*Columella edentula** seg. 2-17, 19, 21-30, 32-38, 40-43, 45-55, 57-76, 78, 80-89, 92, 93, 95-98, 100, 101, 103, 104, 106, 109; H1-9, H11-28, H32-40.
- \*Columella aspera.** 1, 3-5, 7, 10-12, 14, 15, 17, 22-24, 26, 28, 30-34, 36, 39-46, 48-52, 60, 62-65, 67-78, 80-83, 85-92, 94-111; H1-12, H14-20, H25-29, H33-36, H38-40.
- Truncatellina cylindrica.** 28, 30, 33, 54, 61-63, 65, 66, 83, 89.
- Truncatellina callicratis britannica** (= *cylindrica britannica* in Ellis). 3, 9, 10.
- Vertigo pusilla.** 4, 7, 18, 23-28, 32-34, 37, 38, 41, 42, 48-50, 57, 59, 60, 62-73, 75, 87, 88, 91, 95, 98; H8-10, H12, H15, H39.
- Vertigo antivertigo.** 0-4, 6-30, 32-36, 38, 39, 41-43, 45-52, 54-56, 58-67, 69-76, 78-83, 85-89, 95-98, 100-102, 104, 106-108, 110; H1-40.
- Vertigo substriata.** 0, 2-5, 7-9, 11-14, 16-18, 20, 22, 24-30, 32, 33, 35, 37-50, 52, 54, 58-75, 77-81, 83, 85-92, 94-98, 100-110; H1-3, H5, H6, H8-40.
- Vertigo pygmaea.** 0-91, 94, 95, 98, 100-112; H1-40.
- Vertigo moulinsiana.** 4, 8-13, 17, 20-22, 25-29, 40; H2, H9-14, H18-22, H24.
- Vertigo lilljeborgi.** 48, 49, 69, 70, 72-75, 77-80, 87-89, 91, 92, 96-99, 104, 110, 111; H1-3, H9, H15, H16, H27, H29.
- Vertigo alpestris.** 48, 60, 63-65, 67, 69, 70, 89, 103.
- Vertigo geyeri** (= *genesii* in Ellis). 69; H10, H14, H15, H17-19.



- \***Vertigo genesii** (= *parcedentata* (as a fossil only) in Ellis). 66.
- Vertigo angustior**. 25, 27, 60; H1, H3, H9, H13, H16, H19, H27, H28, H34, H39.
- Abida secale**. 1, 3, 6–10, 13–15, 17, 20–24, 30, 33–36, 40, 42, 53, 54, 57, 64, 65, 69, 70.
- Pupilla muscorum**. 0–34, 36–41, 45, 46, 48–54, 56–73, 75, 82, 83, 85, 91, 94, 95, 98, 100, 102, 103, 107–112; H1–3, H5–23, H25, H27, H28, H31, H34, H35, H38–40.
- Leiostyla anglica**. 0–2, 4, 5, 14, 24, 33, 35–38, 40–52, 54, 56–59, 61, 62, 64, 66–76, 81, 83–85, 87, 88, 91, 94–111; H1–40.
- Lauria cylindracea**. 0–112; H1–40.
- \***Lauria sempronii**. 33. Possibly extinct.
- Vallonia costata**. 0–34, 36–41, 45, 47–70, 73, 81–85, 89, 91, 92, 98, 102, 103, 105, 108, 110; H1, H2, H4–11, H13–25, H27, H28, H30, H31, H34, H35, H38–40.
- Vallonia pulchella** seg. 3–38, 40–43, 45, 47, 49, 53–66, 68, 72, 73, 80, 94, 111 (other Scottish records require checking); H1, H2, H6–11, H13–29, H31, H33, H35, H38–40.
- Vallonia excentrica**. 0–42, 44–46, 49–75, 78, 80–85, 88, 91, 97, 98, 100–105, 107–111; H1–29, H31–35, H37–40.
- Acanthinula aculeata**. 0–70, 72–77, 79–83, 85–90, 92, 94–109; H1–29, H31–40.
- Spermodea lamellata**. 14, 15, 24, 33, 39, 45, 46, 48–50, 57, 58, 60, 62–64, 66–77, 79, 80, 82, 83, 86–90, 92, 94–109; H1–3, H5–21, H23, H25–40.
- Ena montana**. 6–8, 11–13, 20, 22–24, 26, 33, 34.
- Ena obscura**. 0–45, 47, 49–70, 72, 77, 79–91, 94–96, 99, 100, 106; H2, H6–11, H13–15, H18–23, H28, H29, H31, H33, H34, H39.
- Punctum pygmaeum**. 0–112; H1–40.
- \***Helicodiscus singleyanus inermis**. 0, 17, 30, 46.
- Discus rotundatus**. 0–111; H1–40.
- Geomalacus maculosus**. H1, H3.
- Arion ater** agg. (including *A. rufus*). 0–112; H1–40.
- Arion lusitanicus** agg. 0–5, 8, 15–17, 37, 38, 41, 42, 44, 45, 48, 49, 58, 61, 64, 66, 69, 77, 109; H3, H16, H21, H33–35.
- \***Arion lusitanicus** Mabilie seg. 3, 4, 15–17, 77.
- \***Arion 'lusitanicus'** Quick. 1–5, 14, 41, 45, 48, 58, 66, 77, 97, 109; H35. I am indebted to Miss Stella Davies for kindly providing the records of this and the preceding species, pending full publication in the *Journal* of her work on the *lusitanicus* complex (see also Cain 1980).
- Arion subfuscus**. 0–112; H1–40.
- Arion circumscriptus** agg. 0–112; H1–40.
- \***Arion circumscriptus** seg. Known to date from 134 vice-counties, and probably ubiquitous.
- \***Arion silvaticus**. Probably ubiquitous (119 vice-counties), though more local than *A. circumscriptus* seg. in most lowland areas.
- \***Arion fasciatus**. 5, 14, 15, 17, 26–30, 32, 36–40, 44, 47, 50, 51, 53–70, 72–77, 79–90, 94–98, 101–109, 111, 112; H28, H31, H34.
- Arion hortensis** agg. 0–112; H1–40.
- \***Arion hortensis** seg. (= *hortensis* form R, Davies 1977). 1–3, 5, 10, 12–17, 20–22, 30, 35, 36, 41, 45, 50, 55, 58, 63, 66; H1, H18. Apparently rare or absent in the northern half of the British Isles.
- \***Arion distinctus** (= *hortensis* form A, Davies 1977). Verified to date from 62 vice-counties, throughout the British Isles. Probably ubiquitous.
- \***Arion owenii** Davies 1979 (= *hortensis* form B, Davies 1977). 2, 3, 21, 22, 41, 72, 75, 77, 83; H34–36, H39, H40.
- Arion intermedius**. 0–112; H1–40.
- Vitrina pellucida**. 0–112; H1–40.



- Semilimax pyrenaicus.** H2, H6, H20, H22, H31, H36, H39, H40.
- Phenacolimax major.** 2, 3, 6, 8, 12, 14, 15, 17, 24, 30, 33–36, 41–43.
- \*Vitreia subrimata.** 64–67, 69.
- Vitreia crystallina** seg. 0–70, 72–99, 101–111; H1–29, H31, H33–40.
- Vitreia contracta.** 0–112; H1–29, H31, H33–40.
- Nesovitrea hammonis** (= *radiatula* in Ellis). 0–112; H1–40.
- Aegopinella pura.** 0–111; H1–40.
- Aegopinella nitidula.** 0–112; H1–40.
- Oxychilus draparnaudi.** 0–46, 48–67, 69–71, 74–77, 80, 83, 85, 86, 88–92, 98, 100, 101, 104, 109–112; H2–23, H26, H27, H29, H31, H36, H38, H39.
- Oxychilus cellarius.** 0–112; H1–40.
- Oxychilus alliarius.** 0–112; H1–40.
- Oxychilus helveticus.** 0–9, 13–61, 63–65, 85, 103–105 (other records from Scotland and the north of England doubtful); H8.
- Zonitoides excavatus.** 0–5, 9–17, 20, 22–24, 27, 30, 32–35, 38–50, 54, 57–64, 66, 67, 69, 70, 72–77, 84, 86–88, 95–105, 108, 110; H1–13, H15–17, H20, H27, H28, H30, H33–36, H38, H40.
- Zonitoides nitidus.** 0–75, 80–83, 86–89, 94–96, 98–103, 105, 106, 110; H1–40.
- Milax gagates.** Records verified post-1930 only. 0–4, 9, 10, 13–15, 17, 22, 25, 27–30, 39, 41, 45, 47, 49, 54, 56, 58, 61–64, 66, 67, 71, 76, 77, 81, 83, 92, 94, 99, 100, 103–105, 109–112; H1, H3–5, H7–10, H12, H15–17, H21, H26–28, H34.
- \*Milax nigricans.** 14. Probably extinct.
- Milax sowerbyi.** Records verified post-1930 only. 1–6, 8–30, 32–37, 39, 41, 42, 45–47, 49, 55–64, 66, 67, 69, 71, 72, 74, 76, 77, 80, 83, 99, 100, 102, 108–110, 112; H1–12, H14–23, H27–31, H37–39.
- Milax budapestensis.** 0–67, 69–72, 75–77, 80, 83, 86, 94, 98–100, 102, 105, 109, 112; H1–11, H13–23, H25–31, H33, H34, H37–40.
- \*Boettgerilla pallens.** 0, 1, 5, 6, 10–12, 14, 17, 27, 30, 37, 41, 49, 55, 57, 58, 63, 64, 69; H38, H39.
- Limax maximus.** 0–112; H1–40.
- Limax cinereoniger.** 2–9, 11–18, 20, 22–24, 30, 33–50, 53–55, 57, 58, 60, 62–73, 77, 83, 86–90, 92, 94–102, 105, 107, 108; H1–3, H6, H9, H11–15, H20, H27, H28, H35, H36, H38–40.
- Limax flavus** agg. 1–3, 5–18, 20–25, 27, 29–42, 44–56, 58–67, 69–77, 81, 83, 85, 92, 94, 95, 100, 102, 109–111 (British records probably mostly *L. flavus* seg.); H1–40 (Irish records mostly *L. grossui* (*maculatus*)).
- \*Limax flavus** seg. Dissection records only. 3, 14, 18, 21, 58, 63, 68–71, 82, 109, 110; H18, H21, H38.
- \*Limax grossui** (= *pseudoflavus* Evans 1978. The correct name for this species is **Limax maculatus** (Kaleniczenko 1851); see Wiktor and Norris 1982). 42, 46, 58, 59, 68, 71, 102; H1, H2, H4–29, H31, H33–40.
- Limax tenellus.** 3, 11, 13–18, 20, 23, 24, 33–37, 39–42, 47, 64–67, 69, 87–89, 91, 92, 95, 96, 102, 107.
- Limax marginatus.** 1–20, 22–58, 60–112; H1–23, H25–40.
- Deroceras laeve.** 0–37, 39–90, 92–101, 103–112; H1–40.
- Deroceras agreste.** 27, 64, 65, 67, 69, 72–77, 79–83, 86–89, 92–95, 97, 105, 108–110.
- Deroceras reticulatum.** 0–112; H1–40.
- Deroceras caruanae.** 0–5, 7–24, 27, 30, 32, 33, 35–50, 52, 53, 55, 57–72, 74–77, 80, 83, 88, 90–92, 94, 96, 107–109, 111, 112; H1–11, H14–23, H25–29, H33, H34, H36–40.



**Euconulus fulvus** agg. 0-112; H1-40.

\***Euconulus fulvus** seg. Few records yet available (40 vice-counties) but probably ubiquitous.

\***Euconulus alderi**. Few records yet available (19 vice-counties). More local than *E. fulvus* seg.

**Ceciloides acicula**. 1-41, 43-45, 49-66, 67, 69; H2, H4-11, H13-19, H21-23, H30-33.

**Cochlodina laminata**. 3-20, 22-43, 50, 51, 53-70, 85, 89, 91; H18, H20, H23, H28-30, H33.

**Macrogastera rolphii**. 3, 6-9, 11-17, 20, 22, 24, 30, 32-38, 40, 53, 54.

**Clausilia bidentata**. 0-77, 79-91, 93-112; H1-40.

**Clausilia dubia**. 15, 60, 63-67, 69, 70, 80.

**Laciniaria biplicata**. 5, 7, 8, 16-18, 20, 21, 29. Many extinctions.

**Balea perversa**. 0-20, 22-43, 45-76, 79-83, 85-89, 91, 93-95, 97-105, 107-112; H1-40.

**Testacella maugei**. 0-9, 11, 13, 17, 21-23, 30, 33-38, 41, 45, 58; H4-7, H11, H21.

**Testacella haliotideia**. 3, 4, 8, 10, 11, 13-18, 20-23, 25, 27-32, 34, 35, 37-39, 43, 54, 56, 58, 62, 66, 73, 80, 83; H1, H3, H5, H9, H10, H15, H21.

**Testacella scutulum**. 0, 1, 3-5, 9-18, 20-24, 27, 28, 30, 32, 37-39, 41, 49, 54-64, 66, 67, 76, 85, 88; H5, H6, H11, H12, H14, H15, H21, H23, H31, H33, H37.

**Bradybaena fruticum**. 15, 16. Possibly extinct.

**Candidula intersecta** (= *caperata* in Ellis). 0-71, 73-86, 90-93, 95-101, 103-112; H1-29, H31, H34, H35, H39, H40.

**Candidula gigaxii**. 6-34, 36, 38-41, 48, 50, 51, 53-56, 58, 59, 61-64, 66, 68, 82; H19, H25.

**Cernuella virgata**. 0-39, 41, 44-46, 48-71, 73, 75, 90, 91, 93, 102, 107-109 H1-26, H31, H32, H34, H37-39.

**Cernuella neglecta**. 16. Extinct.

**Helicella itala**. 1-3, 5-17, 19-34, 36-41, 44, 45, 49-67, 69, 71, 73, 75, 85, 97, 98, 100-105, 108-110; H1-28, H31, H32, H34, H35, H37, H39, H40.

**Trochoidea elegans**. 14, 15, 17.

**Cochlicella acuta**. 0-4, 6, 9, 10, 13-15, 41, 44-46, 49-52, 58, 60, 71, 74, 75, 97, 100-105, 108-110; H1-7, H9-23, H25, H27, H28, H31, H34, H35, H38-40.

\***Cochlicella barbara**. 3.

**Monacha cartusiana**. 11, 13-15, 17, 25.

**Monacha cantiana**. 2-41, 45, 51-57, 61-67, 85, 107.

**Ashfordia granulata**. 0-17, 19-30, 32-34, 37, 40, 41, 44, 45, 48-53, 55-70, 72-76, 79-83, 85, 86, 89-91, 94-105, 108, 110; H1-3, H5, H7-10, H19, H21, H26-28, H34-36.

**Zenobiella subrufescens**. 1-13, 16, 17, 33-37, 39-51, 53, 57-60, 62-64, 66-84, 87-92, 94, 95, 97-107; H1-3, H5-14, H16-18, H20, H21, H27-30, H32, H33, H35-40.

**Hygromia cinctella**. 3.

**Hygromia limbata**. 3, 37.

**Trichia striolata**. 1-111; H1-40.

**Trichia plebeia** (= *liberta* in Ellis). 0, 18-32, 36-40, 42, 43, 47, 53-57, 61, 62, 64, 66.

**Trichia hispida**. 0-91, 93-96, 98-105, 107, 109-111; H1-40.

**Ponentina subvirescens**. 0-4, 45.

**Helicodonta obvoluta**. 11-13.

**Arianta arbustorum**. 1-112; H23, H28-30, H33, H35-40.

**Helicigona lapicida**. 3-27, 29-43, 47, 50, 53-57, 61-65, 80; H5.

**Theba pisana**. 0, 1, 41, 45; H21, H22, H31.

**Cepaea nemoralis**. 0-91, 94, 96-104; H1-40.

**Cepaea hortensis**. 1-73, 75-112; H7-12, H14, H15, H18-23, H27, H31, H34-40.

**Helix aspersa**. 0-76, 78-95, 97-105, 109-111; H1-40.



**Helix pomatia.** 6-8, 12, 14-17, 19, 20, 23, 25, 26, 29, 30, 32-34.

**Margaritifera margaritifera.** 2-4, 34-36, 41, 42, 44-50, 60, 62, 67, 69-77, 86-98, 102, 104-108, 110-112; H1-7, H9, H11-14, H16, H19-21, H26, H27, H30, H31, H33, H34-40. Many extinctions.

**Unio pictorum.** 3, 5-8, 12-34, 36-40, 42, 43, 47, 53-59, 61-64.

**Unio tumidus.** 5-8, 15-24, 27-34, 36-40, 47, 50, 53-59, 61-64.

**Anodonta cygnea.** 6-9, 11-42, 47, 53-66, 72, 73, 85 (other Scottish records doubtful); H8-10, H14-19, H21-33, H37-40.

**Anodonta anatina.** 2, 3, 5-42, 45, 47, 52-68, 70-72, 75, 76, 81-86, 88, 93, 99, 109; H9, H15, H17, H18, H23-25, H28, H33.

**Pseudanodonta complanata** (= *minima* in Ellis). 6, 9, 11-14, 17, 21-25, 27, 28, 30-40, 53, 56, 58, 61, 63, 64.

**Sphaerium corneum.** 0, 3-90, 92, 93, 95, 96, 98, 99, 101, 103, 197-112; H1-40.

**Sphaerium rivicola.** 3, 6-8, 13, 15-24, 30-34, 36-40, 47, 53-59, 61-64.

**\*Sphaerium solidum.** 53, 54.

**Sphaerium transversum.** 6, 8, 17, 21, 23, 24, 32-34, 37-40, 47, 55, 58, 59, 62-64. Many extinctions.

**Sphaerium lacustre.** 0-70, 73-80, 82-86, 88, 93, 99, 106; H2, H4-15, H17, H19-22, H29, H31, H32, H36-40.

**Pisidium amnicum.** 2, 3, 5-43, 45, 47, 50, 53-70, 72, 75-83, 85-88, 93, 99; H2, H4-15, H17-19, H21-25, H30, H31, H33, H36-40.

**Pisidium casertanum.** 0-90, 92-112; H1-40.

**Pisidium conventus.** 49, 69, 70, 87, 88, 96, 97, 99, 108; H1, H33, H35.

**Pisidium personatum.** 0-90, 92-112; H1-40.

**Pisidium obtusale.** 0-76, 78, 81-85, 87-89, 94-106, 108-112; H1-4, H6, H8-36, H38-40.

**Pisidium milium.** 0-90, 92-101, 104-112; H1-40.

**Pisidium pseudosphaerium.** 6, 14, 21, 25, 35, 36, 58, 65; H19, H23, H39.

**Pisidium subtruncatum.** 0-90, 92-104, 106-112; H1-40.

**Pisidium supinum.** 5-7, 12, 13, 15-17, 20-25, 28-32, 36-40, 53, 55-65.

**Pisidium henslowanum.** 2-9, 11-42, 47, 50, 52-70, 72, 76-78, 82-87, 99; H7-11, H13-15, H17-19, H21, H22, H24, H25, H27, H28, H30, H32, H33, H36-40.

**Pisidium lilljeborgii.** 41, 42, 44, 46-52, 59, 60, 62, 64, 67-70, 72-75, 77-81, 83, 85-89, 92, 95-105, 107-112; H1-3, H9, H10, H15-17, H20, H21, H25-28, H30, H33-39.

**Pisidium hibernicum.** 2-9, 11, 12, 14, 15, 17-27, 29-35, 37-50, 52-64, 66-75, 77-80, 84-90, 92, 94-105, 107-112; H1-29, H32-40.

**Pisidium nitidum.** 0-90, 92-112; H1-40.

**Pisidium pulchellum.** 3, 5-17, 19-29, 32, 34, 36, 38, 40-43, 47-50, 52-54, 56, 58, 60, 62-64, 66-70, 72-75, 79, 80, 87-89, 92, 95, 98, 104, 106, 109, 111; H1, H2, H4-13, H15-17, H19, H21-30, H34-39.

**Pisidium moitessierianum.** 2, 6-9, 12, 13, 15, 17, 19-30, 32, 36-40, 47, 53-55, 57, 58, 60, 63, 64; H7, H10, H11, H15, H21, H25, H39.

**Pisidium tenuilineatum.** 6, 8, 11-13, 15, 22-24, 30, 32, 35, 36, 38, 40.

**Dreissena polymorpha.** 3, 6-8, 17, 18, 20-25, 27-34, 36-40, 53-61, 63, 64, 76, 77, 83, 86, 88, 99.



# KERNEY: CENSUS OF NON-MARINE MOLLUSCA

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## COMMUNICATIONS

### EDITORIAL

The Editorial Committee of the *Conchological Society* has decided to introduce, or rather to re-introduce, the publication of short notes to the *Journal of Conchology* under the title of *Communications*. This section is devised to allow the publication of short papers, notes and observations which do not merit the length of a full paper but are nevertheless accounts of original work.

*Communications* will form a section at the end of each issue of the *Journal*, printed in 8 point type (as is this editorial) and should follow the format of those examples below, viz:

A title of not more than one line (50 letters) long; text of up to 1,000 words; no figures, plates or tables; references included in the text in the conventional abbreviated form, omitting reference title; and author's name and address at the end; an abstract is not required.

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B. COLES  
Honorary Editor

## THE OCCURRENCE OF *VERTIGO ANGUSTIOR* IN NORTH LANCASHIRE

On a visit to Gait Barrows National Nature Reserve in North Lancashire on 7 June 1981, some living specimens of a species of *Vertigo* were found which on subsequent examination proved to be *Vertigo angustior* Jeffreys. The only previous record from this area is of fossil specimens of uncertain age from 'cave earth' at Warton Crag (*Lancs. Nat.* 1909, p. 236). In view of the scarcity of this species in the British Isles, especially on the British mainland, the following note gives a description of the habitat where they were found.

Gait Barrows NNR includes about 70 acres of limestone pavement sloping south west to the peaty basin containing Little Hawes Water. The peat overlies deposits of marl and a band of wet meadow and open water transition mire separates the pavement from the pool. Much of the limestone pavement has the typical formation of regular clints and grikes. In other parts it is very massive, with poorly developed grikes, though with a range of other solution features. These features, in the form of hollows or cups of various depths and widths, support a diverse flora of species typical of wet and dry and acid and basic habitats, for example: *Centaureum erythraea* Rafn., *Potentilla erecta* (L.) Räusch., *Molinia caerulea* (L.) Moench, *Juncus articulatus* L. and *Succisa pratensis* Moench—all found in close association here.

The 11 (mostly living) specimens of *V. angustior* were found in these hollows. Most were found in hollows without too lush vegetation, especially among the moss *Homalothecium sericeum* B. & S. This may, however, merely be the easiest type of hollow to search and *V. angustior* may be more widespread.

This habitat is at first glance very unlike those usually recorded for *V. angustior*. Typically it is found in either mossy hollows in sand dunes or in rich marshy meadows (*J. Conch.*, *Lond.* 28, p. 141). In one respect this new habitat resembles the former in being mossy, on the other hand it resembles the latter in that some of the hollows in the limestone pavement contained marshy vegetation. Some of the limestone pavement is covered in dense woodland. *V. angustior* was found in the more open parts where tree development is limited by the absence of deep grikes necessary for their roots. This new habitat fulfils the apparent requirements for *V. angustior* in having high humidity and low vegetation which can be quickly warmed by the sun. The *V. angustior* were found on a warm humid day following overnight rain.

Molluscs found in the immediate area were *Columella aspera* Waldén, *Trichia hispida* (L.) and *Vertigo pygmaea* (Draparnaud), but a full list was not kept. Of these only *V. pygmaea* was actually found in the same hollows with *V. angustior*. One specimen of *V. angustior* has been deposited in the BMNH. It is hoped in future to investigate the distribution throughout the whole reserve and make a more detailed survey of the associated mollusc fauna.

It should be noted that Gait Barrows NNR is a reserve for which written permission is required for a visit. It is hoped that this note will be helpful in the search for living colonies of *V. angustior* in other similar areas in northern Britain.

We should like to thank I. R. Bonner, Regional Officer of the NCC for NW England for permission to visit the reserve and for supplying the list of associated plants, and Dr. M. P. Kerney for confirming the identification of the two species of *Vertigo* and the *Columella*.

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# A NEW BRITISH SITE FOR *THEBA PISANA* (MÜLLER)

Until recently, S.W. Wales, the east coast of Ireland (just north of Dublin) and St Ives, Cornwall, were the only known localities for the xerophilic, calcicolous and frost-tender snail, *Theba pisana*. However, in June 1981 a flourishing colony was found on the north coast of Cornwall, at Treyarnon Bay (grid ref. SW 855740). The snails are established on the rank vegetation surrounding the car park and are especially abundant on the sea-facing side where they extend for some 400 m, halfway to Constantine Bay to the north. A short visit to Constantine resulted in a single specimen being found on the far side of that bay, so it would seem only a matter of time before the species spreads further along the coast. At Treyarnon up to 600 specimens were found clustered on individual plants; the food plant *Beta vulgaris* L. ssp. *maritima* (L.) Thell, being particularly favoured. The typical mode of aestivation with numerous snails clinging to the tall plants was evident, contrasting with the St Ives colony which tends to retire to the base of the vegetation during day-time. Interestingly the snail is also present in the valley at Treyarnon Bay, where it has spread into the marshy habitat and is found on such waterside plants as *Oenanthe crocata* L. and *Phragmites australis* (Cav.). Over seventy flowering plants, mainly maritime species, have been recorded in the locality. On three visits (1 and 15 June, and 3 July), *T. pisana* was noted on the following:

*Aegopodium podagraria* L., *Armeria maritima* (Mill.) Willd., *Calystegia sepium* (L.) R.Br., *Carpobrotus edulis* (L.) N.E. Br., *Cirsium vulgare* (Savi) Ten., *Dactylis glomerata* L., *Daucus carota* L., *Festuca rubra* L., *Galium aparine* L., *Heracleum sphondylium* L., *Lavatera arborea* L., *Nasturtium officinale* R.Br., *Oenanthe crocata* L., *Phragmites australis* (Cav.), *Plantago coronopus* L., *Plantago lanceolata* L., *Raphanus maritimus* Sm., *Rumex crispus* L., *Smyrniololus olusatrum* L., *Sonchus oleraceus* L., *Tamarix anglica* Webb., *Taraxacum officinale* Weber., *Urtica dioica* L.

It is obvious that the coarser, stronger-growing plants are favoured, although the snails are conspicuously absent from such coarse wiry plants as *Ammophila arenaria* (L.), *Agropyron junceaeforme* (A. & D. Löve) and *Carex arenaria* L. Plants associated with *T. pisana* show little obvious damage, despite the very large numbers of snails in the area.

The dunes at Treyarnon are very limited in extent but they are clearly layered, and although *Cernuella virgata*, *Candidula intersecta* and *Cochlicella acuta* are common in the lower horizons, very few living specimens of the last two species were found and none of *C. virgata*. Living *Helix aspersa* are fairly frequent and *Ashfordia granulata* common.

The origin of *T. pisana* as a British species is a mystery; one possibility is that it was introduced to certain sea ports in the process of commerce. To have become so firmly established, one would suppose that it had been at Treyarnon for some considerable time, although shells were not noted in the immediate surface horizons exposed near the shore. The colony at St Ives has been known since 1797 (see *J. Conch.*, *Lond.* **26**, p. 19; **24**, p. 93). Certainly there is no evidence of any conchologists having recorded molluscs at Treyarnon Bay in the past, so the presence of *T. pisana* may have remained unreported for no other reason than this. There is also no evidence that the popularity of this holiday beach adversely affects the snails. A Cornwall County Council aerial survey carried out in 1976 showed 1250 people present on the beach on an August Sunday, with 447 cars in the park; but people obviously keep to the well-trampled paths and tracks, avoiding the rank vegetation and thickets of blackthorn and tamarisk.

A close study of this colony, and a comparison with the St Ives site, could prove most rewarding. The exact extent of the colony needs to be mapped, so that its probable spread can be monitored. The vigour of the snails at Treyarnon appears to be greater than at St Ives, probably because there are no restricting geographical and ecological barriers. In addition to the far greater numbers there is also, not unexpectedly, a wider range of shell pattern and colouring, with many varieties present which do not occur at St Ives. Overall, shell colour and markings tend to be darker and bolder. Among the varieties present, examples of the very attractive *rosaceo-albida* Bourguignat, in which the rosy tint extends outside around the body whorl, were noted.

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# THE BRITISH RECORDS OF *BRADYBAENA FRUTICUM* (MÜLLER)

Both origin and present status of this continental species in Britain remain somewhat mysterious. About 1903 it was found living near Deal (*Proc. malac. Soc. Lond.* **13**, p. 67; specimens in BMNH), in 1908 in a roadside hedge 'between Dover and Lydden' (*ibid.* **12**, p. 124; specimen from Lydden figured in Ellis, *British Snails*, pl. 10), and in 1911 at Penshurst (*Proc. malac. Soc. Lond.* **10**, p. 1; **12**, p. 124); these three records are shown in the 1976 *Atlas* (map 145). Recently I have detected further Kentish specimens of *B. fruticum* in the H. C. Huggins collection (now in the BMNH) labelled 'Kearsney' (V.C. 15; TR 24) and 'Luddesdown' (V.C. 16; TQ 66), all evidently taken live. Dates are not recorded, but are probably around 1920 when Huggins was most active.

In spite of much fieldwork in Kent in recent years the species has not been refound. Mr. Eric Philp and myself have searched for it in hedgerows in the Dover-Kearsney-Lydden area on several occasions without success, and I have also looked around Deal and Luddesdown. Is *fruticum* now extinct in Britain? Possibly the Kentish colonies were only short-lived chance introductions, and it is perhaps significant that other alien molluscs are (or were) known from some of these places: for example, *Cernuella neglecta* from Luddesdown (*Proc. malac. Soc. Lond.* **12**, p. 133;



now extinct), *Trochoidea elegans* near Deal (Walmer), Lydden and Kearsney (*Conchologists' Newsletter* no. 67, p. 114), and – most surprisingly – *Cochlostoma septemspirale* and *C. patulum* at Kearsney (*J. Conch., Lond.* **16**, p. 51; the specimens found by Huggins in 1918 have recently reached the BMNH, and are correctly named).

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## A NOTE ON *HELIX OGDENI* KENNARD & WOODWARD 1914

*Helix ogdeni* was described by Kennard and Woodward in 1914 from a unique specimen collected by Mr. W. E. Ogden 'from a small exposure of Red Crag in a low cliff at Ramsholt, near the River Deben' (*Proc. malac. Soc. Lond.* **11**, p. 155). The specimen was refigured by Harmer in 1916 (*Pliocene Mollusca of Great Britain* **1**, pl. 33, fig. 1), who suggested that it came from the Coralline Crag (Pliocene) rather than the Red Crag (Lower Pleistocene). Kennard and Woodward apparently accepted this view in their subsequent writings, as did Ellis in *British Snails* (1926, p. 231).

In April 1980 Mr. W. E. Ogden donated his large collection of Crag shells, including *Helix ogdeni*, to the British Museum (Natural History) (*The Times*, April 25th 1980). In order to clarify the question of its provenance I wrote to Mr. Ogden, who replied that 'Harmer's suggestion that it might be Coralline was based on a misapprehension as to where the fossil was found. It was NOT, as he says "in a low cliff on the banks of the River Deben" (which is a locality I know and have worked) but in a small pit some half a mile from the river. This pit, which strangely enough yielded little else of interest, was already partially overgrown when we worked it, and is now I fear ploughed over. For the record it was situated approximately half-way between Peyton Hall and Poplar Farm, Grid Ref [TM] 317410. Although the pit was not very productive, the specimens found were all typical Red Crag species and it never entered our minds that it was anything else.'

The specimen (BMNH GG 13364) is a complete, mature shell, but the surface detail has been eroded. Its original ascription to *Macularia* is based on a misunderstanding of earlier literature, and the specimen does not closely resemble recent *Macularia* from S.E. France. Though its taxonomic position remains unclear, the general appearance of the shell is nevertheless that of a south European helicid and it is worthy of note that other land snails having mediterranean affinities occur in the Red Crag (e.g. *Otala lactea*).

I thank Mr. Ogden, of Woodbridge, Suffolk, for recounting the discovery of *Helix ogdeni*, and Mr. J. Cooper (BMNH) for allowing me to examine it.

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## CORNISH STRANDING OF *JANTHINA JANTHINA* (L.) AND *JANTHINA PALLIDA* THOMPSON

Small numbers of *Janthina janthina* (L.) and *Janthina pallida* Thompson were amongst the spectacular wreck of warm-water marine drift animals observed on the Cornish coast in June and July 1981. The buoy barnacle *Lepas fascicularia* Ellis & Solander was also present, but the incursion consisted mainly of the hydroid *Velella velella* (L.) on which *Janthina* preys, and millions of the animals or their scoured floats were seen in shoals off-shore or heaped on the tide-lines. They were particularly common on the north Cornish and north Devon coasts in the sand-catchment areas, and also along the west coast in rapidly diminishing numbers as far as Inverness (sea area S30), where two floats were picked up at Moidart by Mrs. N. F. McMillan, and on the south coast as far as the Yealm Estuary, Devon (sea area SI8). The proportion of predator to prey was surprisingly small and may in part explain the large number and exceptionally large size of the hydroids. A few dozen *Janthina* were found in St Ives Bay (sea area S20) by one of us (J.H.) and a total of nearly a hundred were picked up a few miles to the north by Mrs. S. Thompson at Portreath, Porthtowan and Perranporth. Both species were present at all the localities. Mrs. Thompson noted that the snails were actively feeding on the hydroids, and that during the process they dispensed with the bubble raft, only renewing the bubbles when the food supply was exhausted and when about to drift away, in due course finding fresh prey. The last time that *Janthina* was found this century in any numbers on the British coast was in 1964 when 500 were counted on one section of the beach at Perranporth by Miss N. D. Wood. Previous noteworthy strandings were in 1954 as recorded by D. P. & M. A. Wilson, (*J. mar. biol. Ass. U.K.* **35**: 291–305). At Sennen (sea area SI8) in 1946 T. G. W. Fowler recorded over 100 *J. janthina*; in 1947 'hundreds' of *J. janthina* and *J. pallida*; and in 1949 *J. janthina*, *J. pallida* and *J. exigua* Lamarck (*J. Conch.* **22**: 186 & 268 and **23**: 49). Usually warm-water surface drift of this nature occurs after a prolonged period of westerly winds, but much is yet to be learned about such phenomena and it is always worth recording them in detail.

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## INSTRUCTIONS TO AUTHORS

Authors of papers submitted for publication in the *Journal of Conchology* are urged to pay careful attention to the following notes. Any author who has difficulty in complying with these requests, or has queries concerning manuscripts, should consult the Hon. Editor **before** submitting a manuscript.

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4. Originals of text-figures should be  $1\frac{1}{2}$ –2 times the final size but should not exceed 25 by 36 cm. They should be drawn in Indian ink on clean ground, numbers consecutively, and referred to in the text as “Fig. 1”, etc. Authors are strongly urged to construct text-figures so as to make full use of the page width and to submit a copy reduced to final (published) size wherever possible. Lettering should be legible and not less than 1 mm high after reduction.

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*e.g.*

ELLIS, A. E. 1926. *British snails. A guide to the non-marine Gastropoda of Great Britain and Ireland, Pliocene to Recent*. 275 pp., 14 pls., Oxford.

BROWN, P. and STRATTON, G. B. (Editors). 1965. *World list of scientific periodicals published in the years 1900–1960* (4th Ed.) 3 vols. London.

For periodicals give full title of the article, title of the periodical abbreviated according to the World List (4th Ed.), volume number, page numbers and plates.

*e.g.*

WOODWARD, F. R. 1965. Monograph of the British Lower Tertiary Unionidae, with descriptions of three new species. *J. Conch., Lond.* **25**: 316–330, pls. 22–27.

GOULD, S. J. 1969. An evolutionary microcosm: Pleistocene and Recent history of the land snail. *P. (Poecilozonites)* in Bermuda. *Bull. Mus. comp. Zool. Harv.* **138**: 407–532, 5 pls.

8. Authors may obtain copies of all papers at cost price if ordered from the printers, via the Hon. Editor, when the galley proofs are returned.



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# THE SYNONYMY OF *LIMAX MACULATUS* (KALENICZENKO 1851) WITH NOTES ON ITS EUROPEAN DISTRIBUTION

A. WIKTOR\* and A. NORRIS†

(Accepted for publication 17 October 1981)

**Abstract:** This paper discusses the distribution and synonymy of *Limax maculatus* (Kaleniczenko 1851), in relation to *Limax flavus* Linnaeus 1758. It synonymizes *Limax pseudoflavus* Evans 1978 with *Limax maculatus*.

Quite recently it has turned out that there are two species of *Limax* which are similar to each other in their external appearance, anatomy, and ecological requirements. Until now they have been confused, and both identified as *Limax (Limacus) flavus* Linnaeus 1758. Yet they differ significantly in some characters, notably, that in one of them the spermatheca is attached to the oviduct, and in the other to the penis. When working with large series, differences in their external appearance can also be shown (Likharev and Wiktor 1980).

First, it was necessary to ascertain to which slug the oldest name, i.e. *L. flavus* L., refers. This was possible, although the type probably does not exist. Linnaeus (1758) refers to a still older source, i.e. to Lister's work (1694), on whose frontispiece there is a drawing of the slug, and in his Table 4, fig. 3, there are shown the genitalia. This illustration shows that the spermatheca is attached to the oviduct. Thanks to this it is unequivocally clear to which species the name introduced by Linnaeus should be referred (Likharev and Wiktor 1980). The other species must be designated in some other way. It has been described at least three times, from widely separated areas, as:

*Krynicksillus maculatus* Kaleniczenko 1851: 226, Tab. 6, fig. 2.

Loc. typ.: Kuczukoij=Kuchuk-koy (on the southern shore of the Crimea). There are no data referring to the types.

*Limax grossui* Lupu 1970: 63, Photo 2, fig. 3A, 4, 5B.

Loc. type.: Hagieni (Romania). Holotype in Musée d'Histoire Naturelle 'Grigore Antipa', Bucarest, No 13145.

*Limax pseudoflavus* Evans 1978a: 173.

Loc. typ.: Athlone (Ireland). Holotype: BMNH No 19781 W.

Although the type of *Limax maculatus* is probably non-existent, the drawing of the external appearance (Kaleniczenko 1851, Tab. 6, fig. 2) shows the features characteristic of this slug. We have been able to compare a series of specimens from the Crimea, the Caucasus (and also specimens living synanthropically in greenhouses and cellars in the north and south of the European part of the USSR), and from Turkey, Bulgaria and Ireland. This comparison reveals not only that *L. grossui* is a synonym of *L. maculatus* (as has already been demonstrated by Wiktor and Likharev 1980), but that *L. pseudoflavus* is also a synonym. The features differentiating *L. grossui* and *pseudoflavus*, enumerated by Evans (1978), viz. the C-like curvature of the penis, the length of the spermatheca duct, and other details of its anatomy, depend largely on the level of sexual maturity of the slug and on the manner of its

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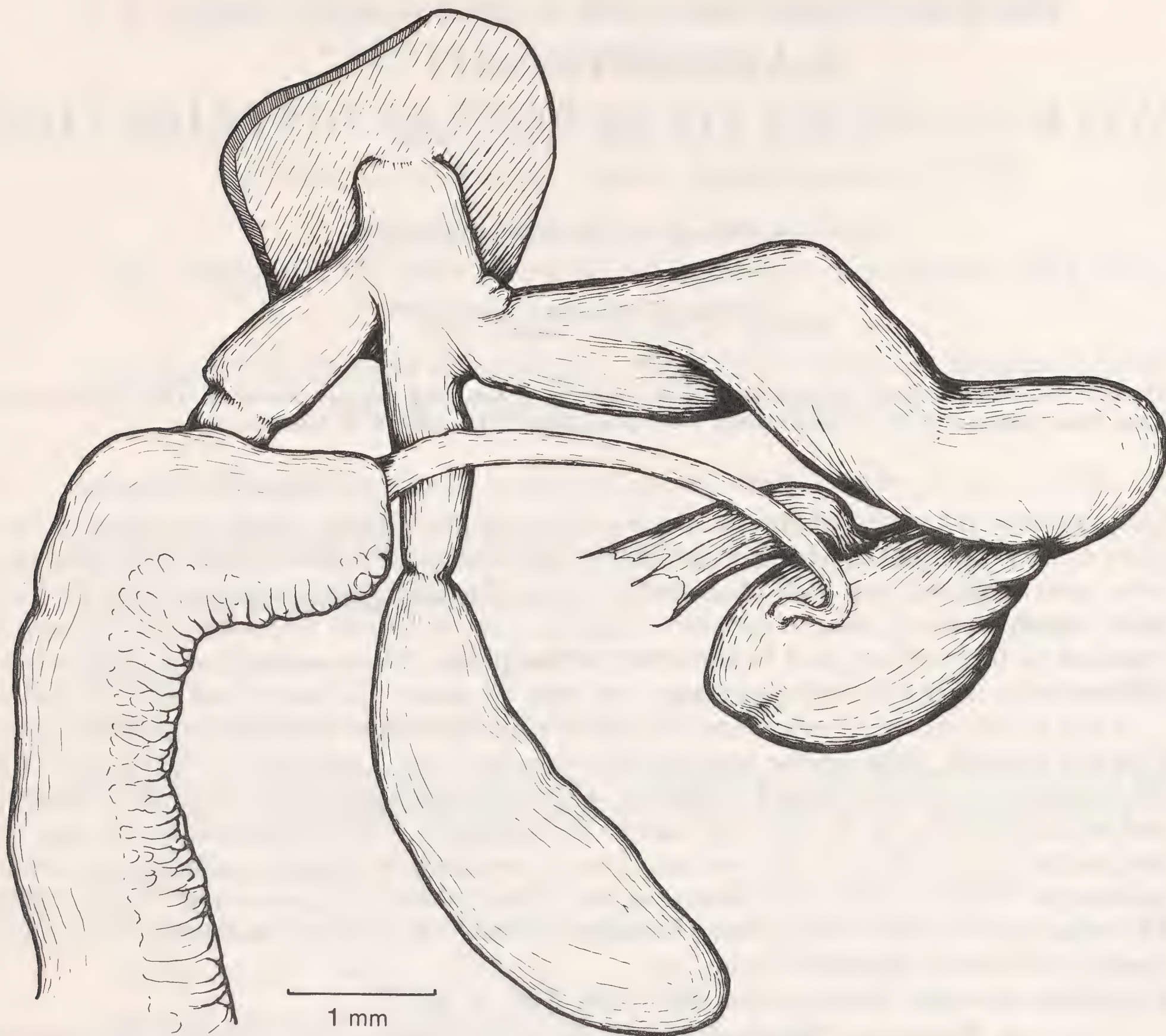


Fig. 1. *Limax maculatus* (Kal.) Crimea (U.S.S.R.) Verkhnyaya Krimea—Zovka. Leg. Shapiro. 1.9.1974.

preservation, so it is false to consider them to be taxonomic characters. *L. pseudoflavus* therefore also turns to be a junior synonym of *L. maculatus* (Kaleniczenko)<sup>1</sup>. Information on *L. maculatus* then, should additionally be looked for under the designations *L. grossui*, *L. pseudoflavus* and, in part, *L. flavus* (see also Evans 1978 a & b; Likharev and Wiktor 1980, p. 284).

It is worth pointing out that *Limax maculatus* can usually also be distinguished from *L. flavus* by the external appearance. In *L. maculatus* dark pigment reaches, on the sides of the body, down to the edge of the foot, while in *L. flavus* there is a wide pale zone devoid of pigment above the edge of the foot. Also, *L. maculatus* is darker, has a more distinct pattern on its body and usually matures when smaller in size.

*Limax maculatus* is a forest species. It is native in the areas situated on the Black Sea; the Crimea; the Caucasus, and probably also Turkey, Romania and Bulgaria. It easily adapts

<sup>1</sup>Not invalidated by *Limax maculatus* Nunneley 1837 (= *L. maximus* L. 1758), a name which must be rejected as not fulfilling the requirements of rule 11(d) of the ICZN code.





Fig. 2. Known distribution of *Limax maculatus*. Isolated introductions north of main area of distribution shown as dots.

itself to environments altered by man, and is found, among other places, in greenhouses and cellars. This type of occurrence is also found within the areas where it is indigenous, i.e. where it lives in unaltered biotypes. It has been probably brought as a synanthrope to Ireland, to Great Britain, and to some parts of the U.S.S.R. (see above). It probably occurs in France, as is evidenced by the drawing in Moquin-Tandon (1855, Pl. 3, figs. 3 and 6). It can be expected to be discovered in other regions of Europe as an introduced synanthropic species.

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# AN ANNOTATED CHECK-LIST OF THE NON-MARINE MOLLUSCA OF THE PITYUSE ISLANDS, SPAIN

C. R. C. PAUL\*

(Accepted for publication 17 October 1981)

*Abstract:* 36 terrestrial and 12 fresh or brackish-water molluscs are confirmed living in Ibiza and Formentera. The identity of the succineid has not been authenticated anatomically and remains doubtful, as do three additional records, one of a slug and two of freshwater snails. *Punctum* (*Toltecia*) *pusillum* (Lowe) and *Cecilioides acicula* (Müll.) are recorded from Ibiza for the first time.

## INTRODUCTION

This paper is intended to provide an up to date check-list of the Recent non-marine Mollusca found on the Spanish Mediterranean islands of Ibiza and Formentera, collectively known as the Pityuse Islands to distinguish them from Mallorca and Menorca which form the Balearic Islands proper. Knowledge of the non-marine molluscs of the Pityuse Islands has grown slowly and this paper adds a further two species not previously recorded from them. Very little indeed has been written in English about all molluscs from the Spanish Mediterranean islands and it is hoped that this paper will also act as an introduction to the literature, which is extensive but difficult to trace—the more so because one major bibliographic reference source has entirely overlooked the *Boletín de la Sociedad de Historia Natural de Baleares*, in which most of the more recent papers have been published. For non-marine molluscs the most important references are: Bofill and Aguilar-Amat 1924; Jaeckel 1952; Sacchi 1954; Gasull 1964a, 1965, 1969, 1979, Gasull and Alena 1969, and Schröder 1978a, b.

The check-list is restricted to confirmed records based on my own collecting in 1975 and 1977, together with records of Luis Gasull over the last 45 years and the recent list of Schröder (1978a) for Formentera. 36 land snails and 12 fresh or brackish-water molluscs, including one species of *Pisidium*, are accepted, with three additional doubtful records. My own localities were recorded on a 1 km grid. Records for 76 squares were obtained, 73 on Ibiza and 3 on Formentera (Fig. 1). As an approximate indication of abundance, the list includes the number of 1 km square records for each species. Maximum diversity at one locality was 25 species, but only three localities had 20 or more species and all included several freshwater forms. Most sites yielded between four and nine species.

To save space all the records include information in the following sequence: specific name (number of 1 km square records, which islands they are recorded from, viz. I=Ibiza, F=Formentera), first record and (reference if different). Comments.

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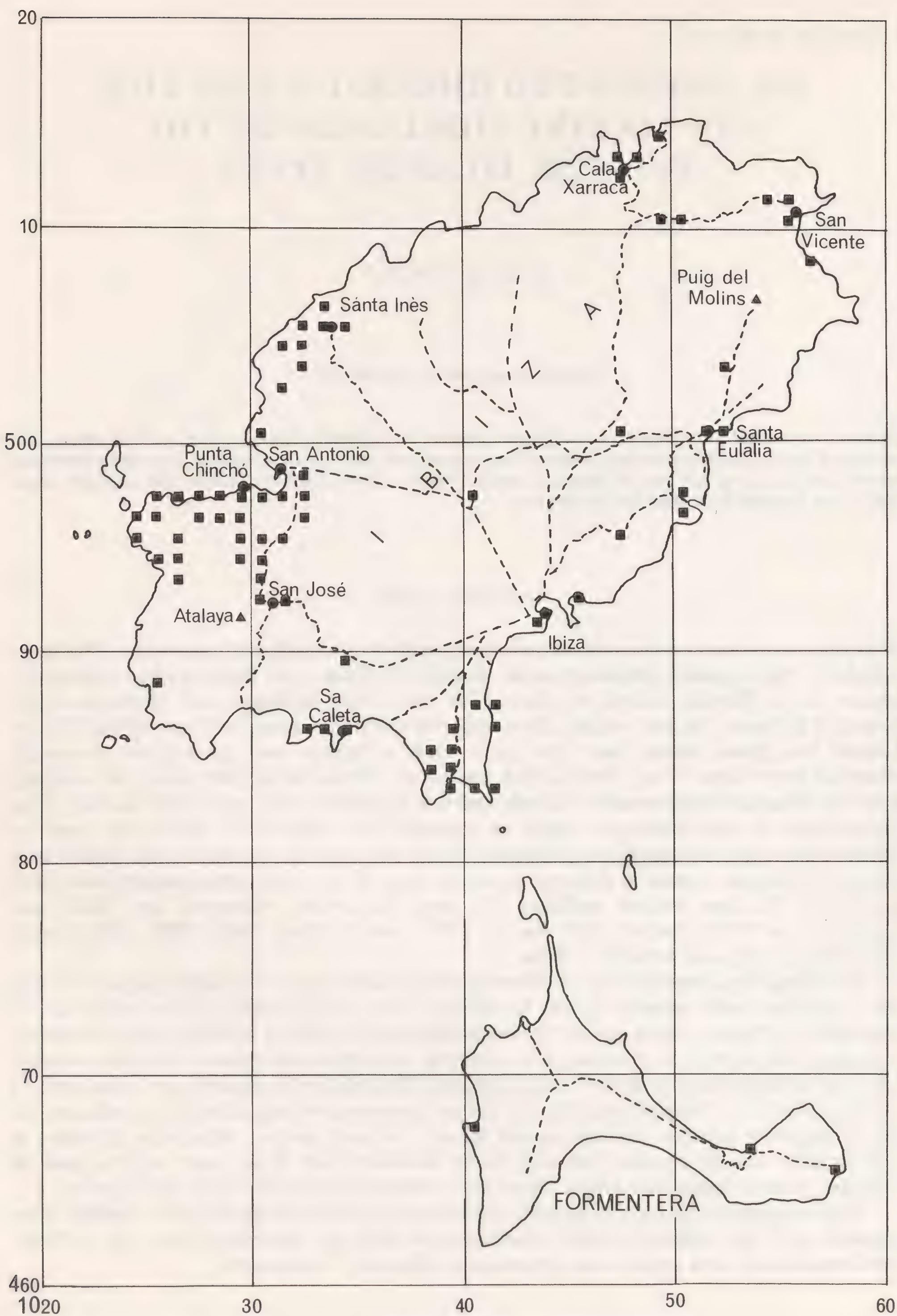


Fig. 1. Map of the main Pityuse Islands to show Spanish Grid and collecting stations.



## LAND SNAILS

*Pomatias elegans* (Müller) (O; I). Gasull 23.vii.47 (Gasull 1964a, p. 66). Confined to a small area on the north side of the valley leading to San Vicente.

*Oxyloma pfeifferi* (Rossmässler) (O; I). P. Font Quer, 15.iii.19 (Gasull 1965, p. 110). Bofill and Aguilar-Amat (1924, p. 33) recorded two juveniles of *Succinea putris* (L.) collected by Font Quer, a record repeated by Jaekel (1952, p. 90). However, Gasull (1965, p. 110) considered the specimens to be juvenile *O. pfeifferi* and he added more records of his own. Margalef (1951, p. 56) records *S. elegans* Risso [= *O. sarsi* (Esmark)]. No anatomical data have been published. It is certain that at least one succineid species lives on Ibiza, but knowledge of the anatomy is required to confirm which one.

*Truncatellina callicratis* (Scacchi) (1; I). Gasull 25.iii.77 (Gasull 1979, p. 11). Gasull discovered this species at Santa Eulalia three days before I located it at Cala Xarraca. There is considerable variation in size (Fig. 2), but most examples have three distinct teeth in the aperture.

*Vertigo antivertigo* (Draparnaud) (O; I). Gasull 12.ii.68 (Gasull 1969, p. 66). The original record stated that the identity was confirmed by H. W. Waldén, but surprisingly the record was not mentioned in Gasull's later work on 'micro-pulmonates' (Gasull 1979).

*Granopupa granum* (Draparnaud) (2; I, F). Hidalgo (1878, p. 241). Locally abundant, but not easy to find. Specimens I have from Cala Xarraca are about half the size of others from France.

*Lauria cylindracea* (da Costa) (2; I). Sacchi (1954, p. 30). Uncommon. Sacchi mentions one locality, Atalaya (? the one near San José); Gasull (1979, p. 10) added San José and Santa Eulalia, and I have found it at Cala Xarraca and near Chinchó on the south side of San Antonio Bay. These localities are widely separated and the species may well have been overlooked.

*Punctum (Toltecia) pusillum* (Lowe) (1; I). C.R.C.P., 28.iii.1977. Three typical examples found by sieving at the foot of a drystone retaining wall on the edge of a watercourse just upstream from the beach at Cala Xarraca.

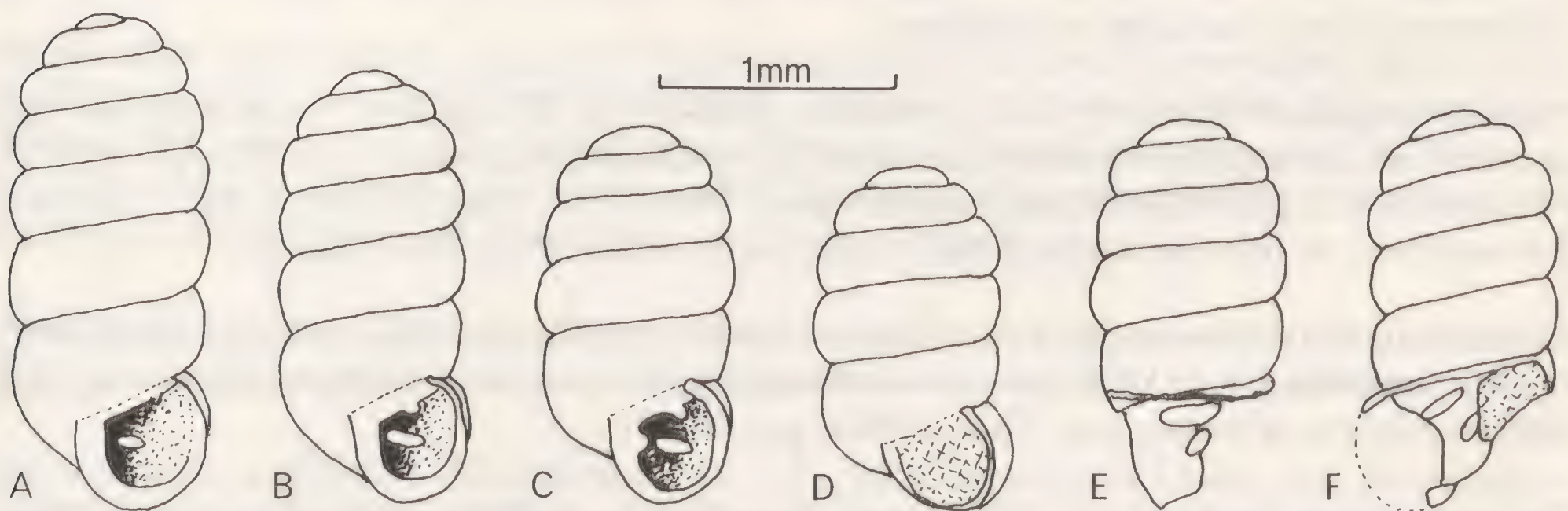


Fig. 2. *Truncatellina callicratis* (Scacchi), Cala Xarraca, Ibiza, to show variation in size and apertural denticles.



*Vitrea gasulli* Riedel & Paul 1978 (3; I). Bofill and Aguilar-Amat (1924, p. 17) record a single example of '*V. crystallina*' collected by E. Gros at Santa Agnès (now Santa Inès). This species is otherwise unknown in the Balearics and Pityuses and all other examples of *Vitrea* from Ibiza belong to the endemic species *V. gasulli*. Otherwise this species was first discovered by me at Santa Eulalia on 9.iv.75. Gasull (1979, p. 17) records it from Santa Eulalia and San José and I added Sa Caleta and Cala Xarraca in 1977. Again this species is apparently widespread and quite likely under-recorded.

*Oxychilus pityusanus* Riedel 1969 (12; I, F). Possibly first recorded from both islands by J. Bernström in 1933 (Riedel 1969). Endemic to the Pityuse Islands, quite widespread, but not common.

*Milax gagates* (Draparnaud) (?3; I). Possibly first recorded by S. Jaeckel (1952, p. 85). None of my specimens was dissected and one record was based on a juvenile. Gasull and Altena (1969, p. 125) record this species from San José. Although they give no anatomical information, all Gasull's slug material was dissected by Altena and is now deposited in the National Museum of Natural History in Leiden.

*M. nigricans* (Philippi) (O; I). Possibly first recorded by Jaekel (1952, p. 85) as *M. gagates*. Gasull and Altena (1969, p. 127) record it from two localities, San Antonio and Ibiza Town.

*Limax majoricensis* Heynemann (O; I). Gasull and Muntaner, 22.xi.55 (Gasull and Altena, 1969, p. 129). Heynemann's original material came from Mallorca, as the trivial name implies.

*L. flavus* (L.). (O; I) Gasull and Mercadal, 21.v.51 (Gasull and Altena 1969, p. 130).

*L. valentianus* Férussac (O; I, F). Gasull, 20.vi.61 (Formentera) and 11.ii.68 (Ibiza), (Gasull and Altena 1969, p. 131).

*Ferussacia follicula* (Gmelin) (15; I, F). Hidalgo (1878, p. 241). Widely distributed, but under-recorded due to its cryptic habits. Usually found under stones.

*Ceciloides acicula* (Müller) (1; I). C.R.C.P., 28.iii.77. The specimens, which are all damaged, are consistently a little narrower than British examples, but are otherwise identical. It seems likely that the Cala Xarraca population is merely a slender form of *C. acicula* which is also recorded from the Balearic Islands.

*Rumina decollata* (L.) (60; I, F). Apparently first recorded by Hidalgo (1878, p. 239). Widespread and abundant everywhere.

*Papillifera papillaris* (Müller) (O; I). Salvador (1886–90, p. 33) apparently first recorded this species from the capital, whence it has since been recorded repeatedly (e.g. Hidalgo 1878, p. 242; Bofill 1918, p. 218; Bofill and Aguilar-Amat 1924, p. 32; Gasull 1964a, p. 62). However, it is confined to this one locality and to the north side of Puig dels Molins.

*Cernuella virgata* (da Costa) (49; I, F). First recorded by Dohrn and Heynemann (1862, p. 102) as *Helix variabilis* Drap. Widespread and abundant. Very variable and previously recorded under a variety of names (see Gasull 1965, pp. 26–7).

*Helicopsis apicina* (Lamarck) (O; I). Gasull. 15.ix.35 (Gasull 1965, p. 37). Known only from the north side of Puig dels Molins.



*Trochoidea (Trochoidea) elegans* (Gmelin) (30; I, F). First recorded by Dohrn and Heynemann (1862, p. 102) as *Helix terrestris* Chemnitz. Widespread and common, but surprisingly rare in the southwest of Ibiza west of San Antonio. Most specimens I collected have the wide spiral angle typical of the form *scitula* Cristofori & Jan.

*T. (T.) trochoides* (Poiret) (O; I). First recorded by Bofill (1918, p. 294) as *Helix conica* Drap. Gasull (1965, p. 49) presents a map of localities for this species. According to him, *T. trochoides* is more common than *T. pyramidata*, but only occurs in the southern two-thirds of Ibiza and not at all on Formentera. All the material I collected was *T. pyramidata*.

*T. (T.) pyramidata* (Draparnaud) (15; I, F). First recorded by Hidalgo (1878), p. 228). Gasull (1965, p. 45) maintains that *T. pyramidata* only occurs on the extreme south of Ibiza and on Formentera. However, most of my localities lie just south of the Bay of San Antonio in southwest Ibiza.

*T. (Xerocrassa) ebusitana* (Hidalgo) (30; I, F). First recorded by Hidalgo (1869, p. 19). Gasull (1964b, pp. 8–19) gives a full account of this and the next endemic species. The shells are very variable and Jaeckel (1952) has described many sub-species from the smaller islands of the Pityuse Group. Schröder (1978b) has added anatomical information for some of these forms.

*T. (X.) caroli* (Dohrn & Heynemann) (56; I, F). First recorded by Dohrn and Heynemann (1862, p. 107). Both these endemic species are widespread and common. *T. (X.) caroli* appears to be more common on sand dunes near coasts.

*Cochlicella acuta* (Müller) (35; I, F). First recorded by Hidalgo (1878, p. 240) as *Bulimus acutus*. Common and widespread.

*C. conoidea* (Draparnaud) (27; I, F). First recorded by Dohrn and Heynemann (1862, p. 108) as *Helix solitaria* Poiret. Much more common in the south and west of Ibiza.

*C. barbara* (L.) (O; I). Gasull (1965, p. 58) records this species, as *C. ventricosa* (Draparnaud), from San Antonio, collected 20.iii.52. Otherwise it is unknown from Ibiza. Earlier records of *C. barbara* (e.g. Bofill 1918, p. 214, Bofill and Aguilar-Amat 1924, p. 25) refer to *C. acuta* (Müller).

*Caracollina lenticula* (Férussac) (12; I, F). First recorded by Dohrn and Heynemann (1862, p. 102) as *Helix lenticula*. Widespread, but commonly overlooked due to its cryptic habits. Usually found under stones.

*Iberellus minoricensis* (Mittre) (24; I, F). First recorded by Dohrn and Heynemann (1862, p. 109) as *Helix balearica* var. *companyonii*. Widespread, common and very variable. *Helix companyoni* Aleron 1837, which was described from the Pyrénées Orientales, is a *nomen nudum*. The next available name is *Helix minoricensis* Mittre 1842. It is highly likely that the forms from Menorca are indeed conspecific with those from the Pityuse Islands.

*Theba pisana* (Müller) (61; I, F). First recorded by Dohrn and Heynemann (1862, p. 108) as *Helix pisana*. Widespread and abundant. Typically aestivates high on vegetation.

*Sphincterochila candidissima* (Draparnaud) (5; I, F). First recorded by Dohrn and Heynemann (1862, p. 101) as *Leucochroa candidissima*. Restricted to the south coast of Ibiza and Formentera where it sits out in the sunshine, relying on the opaque white shell to reflect the sun's rays.



*Eobania vermiculata* (Müller) (68; I, F). First recorded by Dohrn and Heynemann (1862, p. 108) as *Helix vermiculata*. The most common and obvious species. Widespread and variable in size and coloration.

*Otala punctata* (Müller) (45; I, F). First recorded by Dohrn and Heynemann (1862, p. 108) as *Helix lactea* var. *punctata*. Widespread and very common. Not easily overlooked due to its size. The related species, *Otala lactea* (Müller), has been recorded repeatedly from Ibiza (e.g. Salvador 1859, Dohrn and Heynemann 1862, Hidalgo 1878, Jaeckel 1952) yet there have been equally repeated denials that it occurs in the Pityuse Islands (e.g. Bofill and Aguilar-Amat 1924, p. 27, Sacchi 1954, p. 30, Gasull 1965, p. 80) and I have not seen a single example. I am personally convinced that earlier records were based on *O. punctata*.

*Helix (Cornu) aspersa* Müller (21; I, F). First recorded by Bofill (1918, p. 216). Widespread, but not that common.

#### FRESH AND BRACKISH-WATER SPECIES

*Melanopsis dufourei* (Férussac) (3; I). First recorded by Bourguignat (1884, p. 105) as *M. etrusca* Villa (ms). Locally common in streams that are fairly constant. Clings to rocks in rapids. Like most freshwater species in Ibiza, it is largely confined to the very few constant water courses, but has been artificially spread by irrigation schemes.

*Amnicola similis* (Draparnaud) (3; I). Gasull, 24.iv.46, (Gasull 1965, p. 144) Abundant, but local. Gasull states that forms from Ibiza differ from the typical form by being smaller, having more flattened whorls and a larger and more oval aperture.

*Hydrobia acuta* (Draparnaud) (O; I, F). J. Cuerda, 15.ix.35, Gasull (1965, p. 146). Apparently not common. In ditches.

*Bithynia leachii* (Sheppard) (3; I). First recorded by Bofill (1918, p. 206).

*Ovatella myosotis* (Draparnaud) (O; I, F). First recorded by Hidalgo (1878, p. 244).

*Physa acuta* Draparnaud (2; I). First recorded by Salvador (1886–90, p. 32).

*Lymnaea (Galba) truncatula* (Müller) (2; I). Bofill (1918, p. 219).

*Lymnaea (Radix) peregra* (Müller) (2; I). Gasull, 9.ii.60 (Gasull 1965, p. 119) as *L. (R.) ovata* (Draparnaud).

*Planorbis planorbis* (L.) (2; I). Apparently first recorded by Jaeckel (1952, p. 85) as *Tropidiscus planorbis* var. *submarginatus* Cristofori & Jan.

*Gyraulus laevis* (Alder) (2; I). Gasull, 22.vii.47 (Gasull 1965, p. 140).

*Ancylus fluviatilis* Müller (2; I). Gasull, 24.vii.47 (Gasull 1965, p. 132).

*Pisidium casertanum* (Poli) (O; I). According to Gasull (1969, p. 70) recorded by Aspeitia Moros (1933) from Ibiza Town and San Antonio.



## DOUBTFUL RECORDS

*Milax sowerbyi* (Férussac). Recorded by Jaeckel (1952, p. 85) without anatomical information and not confirmed by Gasull and Altena (1969).

*Isidora contorta* (Michaud). Recorded by Sacchi (1954, p. 9) as *Bullinus contortus*.

*Anisus spirorbis* (L.). Bofill (1918, p. 219) and Bofill & Aguilar-Amat (1924, p. 33) record many examples collected by E. Gros and P. Font Quer from near the Capital, but there are no subsequent records.

## REMARKS

The more thoroughly the fauna of any locality is studied, the more difficult it becomes to discover species new to the area. One therefore expects most of the species present to be recorded early in the history of collecting with a few rarer, more local or minute species added later on; in the Pityuse Islands the pace of discovery has not yet declined. While this is partly due to the increased interest in the fauna of the islands since the last war, it also seems likely that we have yet to produce a definitive faunal list and that additional species will be discovered by further intensive collecting.

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# OCCURRENCE OF *ELYSIA SERCA* MARCUS IN FLORIDA, WITH NOTES ON THE SYNONYMY AND BIOLOGY OF THE SPECIES

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*Abstract:* *Elysia clena* Marcus and Marcus 1970 is synonymized with *E. serca* Marcus 1955 on the basis of morphological and biological observations. Radular morphology and pattern of dorsal veins show overlap in various geographical populations in Florida, and reproductive anatomy does not show sufficient differences to validate separation of two species. *E. serca* feeds on 3 genera of seagrasses, *Halophila*, *Halodule*, and *Thalassia*. The shape of radular teeth, buccal anatomy, and pattern of dorsal veins are very similar to *E. catulus* (Gould 1870), the only other ascoglossan reported to feed on seagrasses.

## INTRODUCTION

Only three species of *Elysia* have been described in which the teeth are shaped with the cusps nearly perpendicular to the bases. These are *Elysia catulus* (Gould 1870) from the Atlantic coast of northern U.S.A., *Elysia serca* Marcus 1955 from Brazil, and *Elysia clena* Marcus and Marcus 1970 from Curaçao, Barbados and Florida. *Elysia serca* has roughly denticulate teeth (Marcus 1955), and its food was thought to be *Ulva* (Hosoe 1956, Marcus 1957) and *Sargassum* or *Padina* (Marcus 1957). In *Elysia clena*, only the smallest teeth in the ascus have denticles (Marcus and Marcus 1970), or they are completely smooth, as in the specimens from Florida (Marcus 1972a). Nothing has been mentioned about the food of this species, but all the specimens from Barbados (N=26) were collected from *Thalassia* (Marcus and Hughes 1974). The teeth of *Elysia catulus* are also completely smooth (Marcus 1972b), and the food of this species is *Zostera marina* L. (Clark 1975).

This study presents collection data for specimens of *Elysia serca* from Florida. Based on morphological and biological observations, *E. clena* is synonymized with *E. serca*. Feeding method and food spectrum are described.

## MATERIAL AND METHODS

In the period from October 1977 to June 1980 *Elysia serca* was collected at several locations in Florida. These are shown on Fig. 1. Other collection data are shown in Table 1.

Feeding was observed as described by Jensen (1981). The lengths of a number of animals were measured by ocular micrometry, and the number of dorsal veins counted. A few specimens were fixed in 4% neutral formaldehyde in seawater, dehydrated in ethanol, and embedded in paraffin. Sections were cut at 5 µm, and stained in either haematoxylin/eosin or

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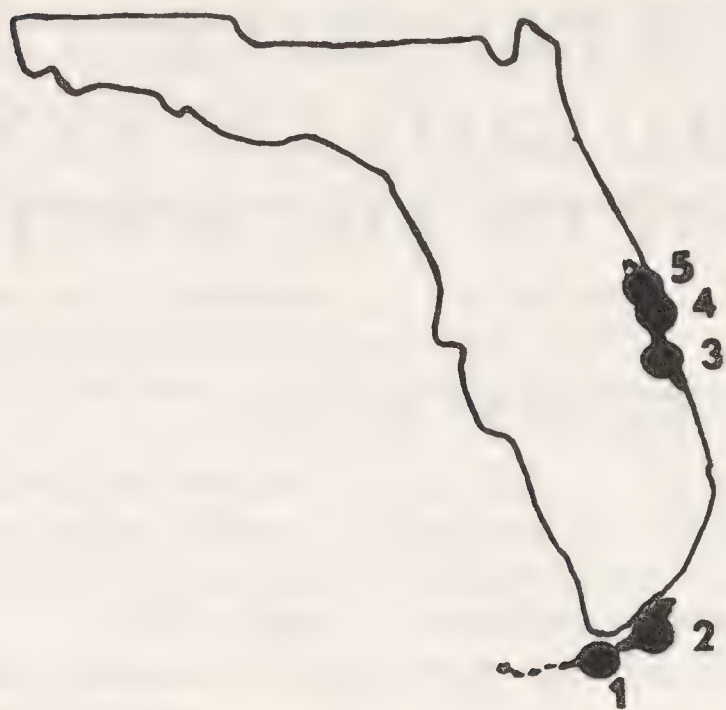


Fig. 1. Map of Florida showing locations for collections of *Elysia serca*. 1—Long Key; 2—Key Largo; 3—Fort Pierce Inlet; 4—Banana River (east of Merritt Island); 5—Indian River (northern tip of Merritt Island).

TABLE 1

Collection data for *Elysia serca* from Florida.

Location	Substrate	Season
Point Elizabeth, Key Largo; Long Key	<i>Thalassia</i> , <i>Halodule</i>	winter—early spring
Tidal canal, Key Largo	<i>Halodule</i> , <i>Halophila</i>	fall—early spring
Fort Pierce Inlet	<i>Thalassia</i>	fall
Banana River	<i>Halophila</i>	spring—early summer; fall
Indian River	<i>Halophila</i>	spring—early summer

Mallory’s trichrome stain (Gray 1964). Radular mounts were made as described by Jensen (1981). The teeth were counted. The dimensions of cusps and bases of the teeth were measured by ocular micrometry and compared to the size of the buccal mass, and the results from different populations were compared.

RESULTS

*Morphology:* Specimens of *Elysia serca* from Key Largo and Long Key all had smooth radular teeth, as mentioned for *E. clena* from Florida (Marcus 1972a), but the pattern of the dorsal veins was that of *E. serca* (Marcus 1955, 1980). The animals from Fort Pierce Inlet were all juvenile when collected and the pattern of dorsal veins was that of *E. clena* (Marcus and Marcus 1970, Marcus 1980), but after several weeks of growth in the laboratory this pattern had changed into that of *E. serca* (Fig. 2). The teeth of these animals were also completely smooth. Juvenile animals from the Banana River had dorsal veins in the pattern of *E. clena* (Fig. 3) whereas adult animals had the pattern of *E. serca*. The teeth of all investigated specimens were completely smooth (Fig. 4A and B). The specimens from the Indian River all had coarsely denticulate teeth, as originally described for *E. serca* (Marcus



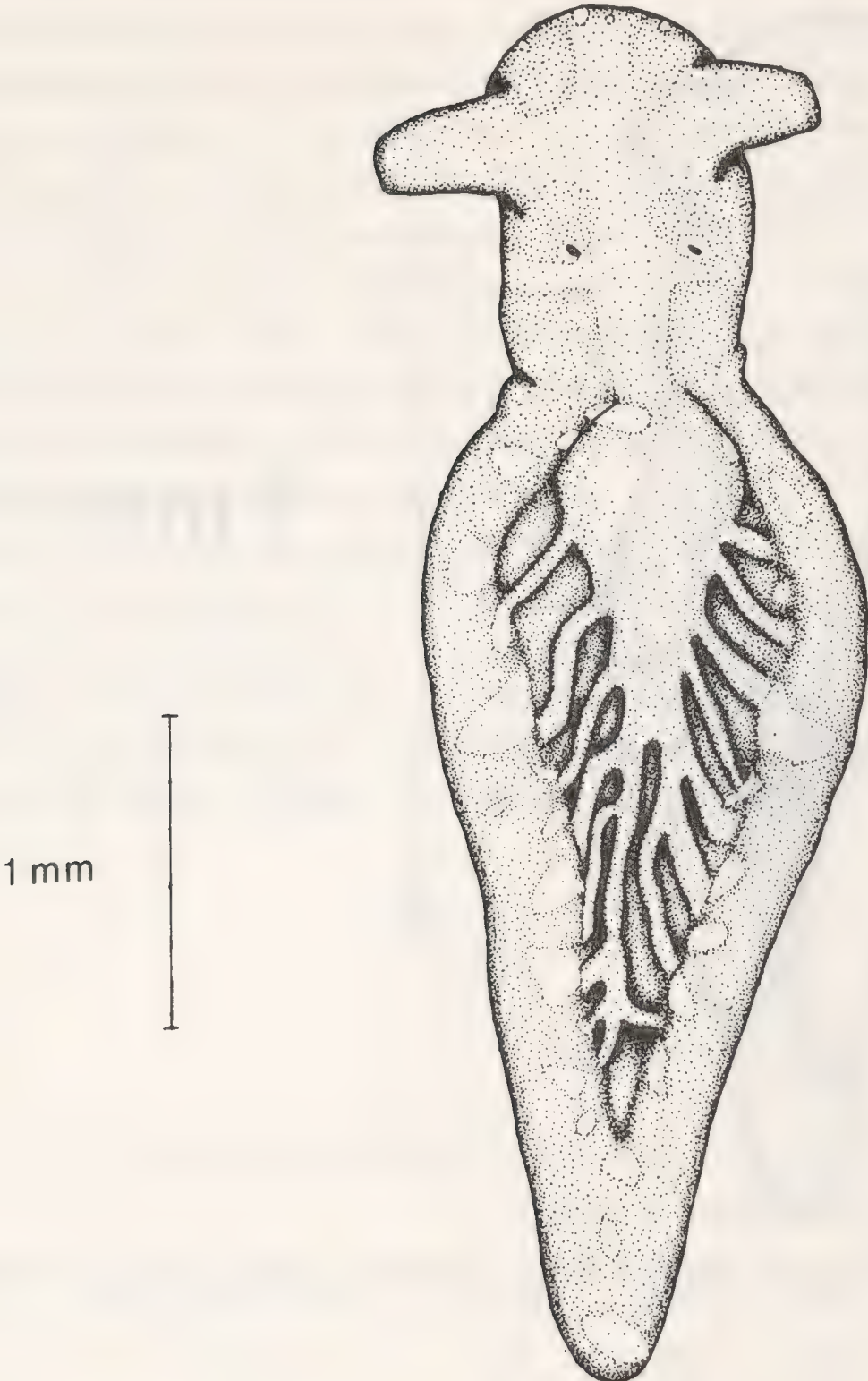


Fig. 2. *Elysia serca*. Adult animal collected as a juvenile at Fort Pierce Inlet and allowed to grow for several weeks in the laboratory. Animal drawn with camera lucida while relaxed in 8%  $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$  in seawater.

TABLE 2

Number of dorsal veins of *Elysia serca* from different populations.

Population	Food	Body length, mm	Number of veins on			
			right side		left side	
			unbranched	branched	unbranched	branched
Indian River	<i>Halophila</i>	5.59	5	2	4	1
		4.29	4	2	4	2
		3.64	3	1	3	1
		2.91	3	2	3	2
		2.37	3	2	2	2
		2.05	4	1	3	1
		1.73	4	0	4	0
Key Largo	<i>Halodule</i>	4.0	2	2	4	2
Fort Pierce	<i>Thalassia</i>	4.2	4	2	3	3
Banana River	<i>Halophila</i>	1.5	2	0	3	0
		1.5	3	0	3	0
		1.5	2	1	2	1



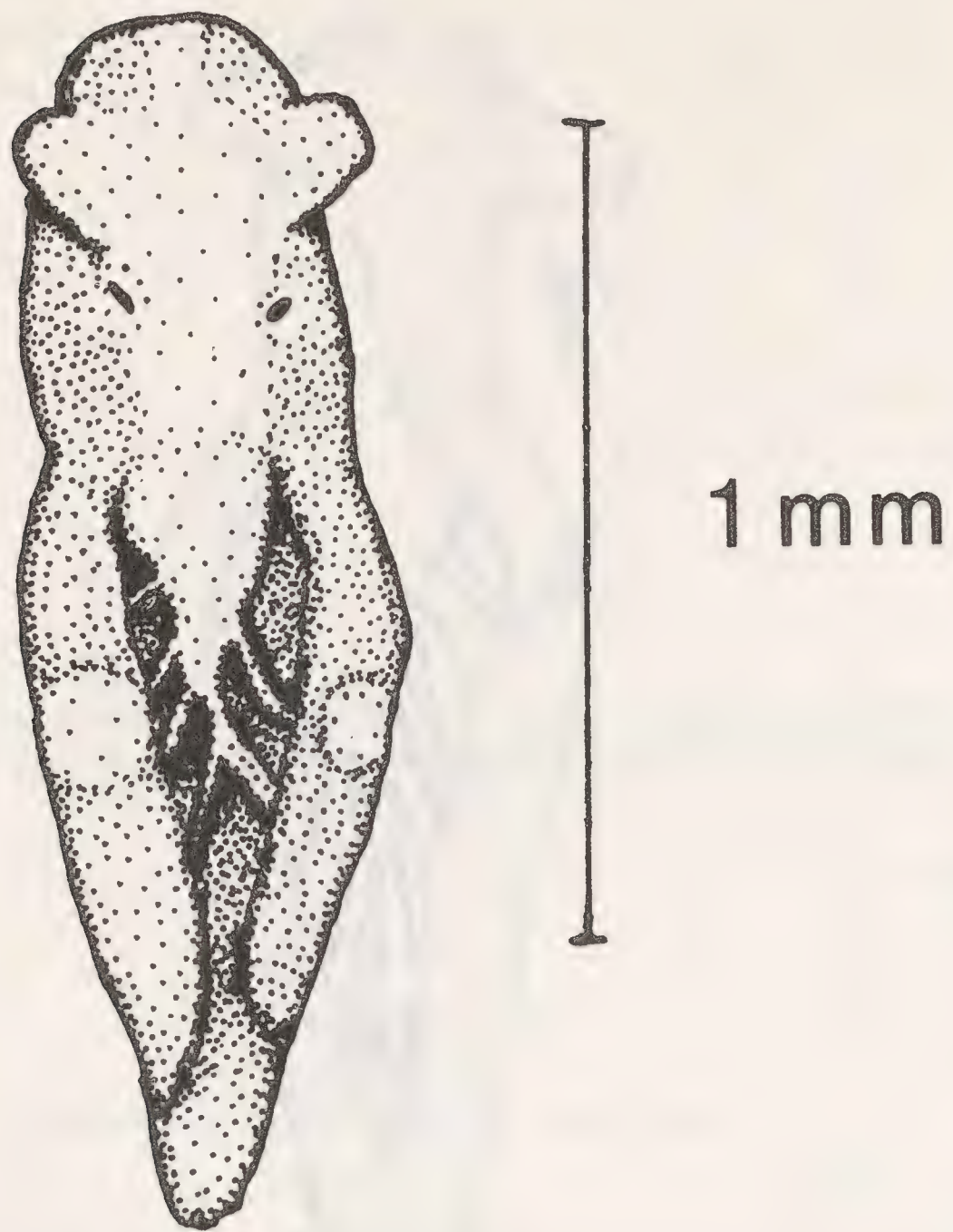


Fig. 3. *Elysia serca*. Juvenile animal from the Banana River. Camera lucida drawing of animal relaxed in 8%  $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$  in seawater.

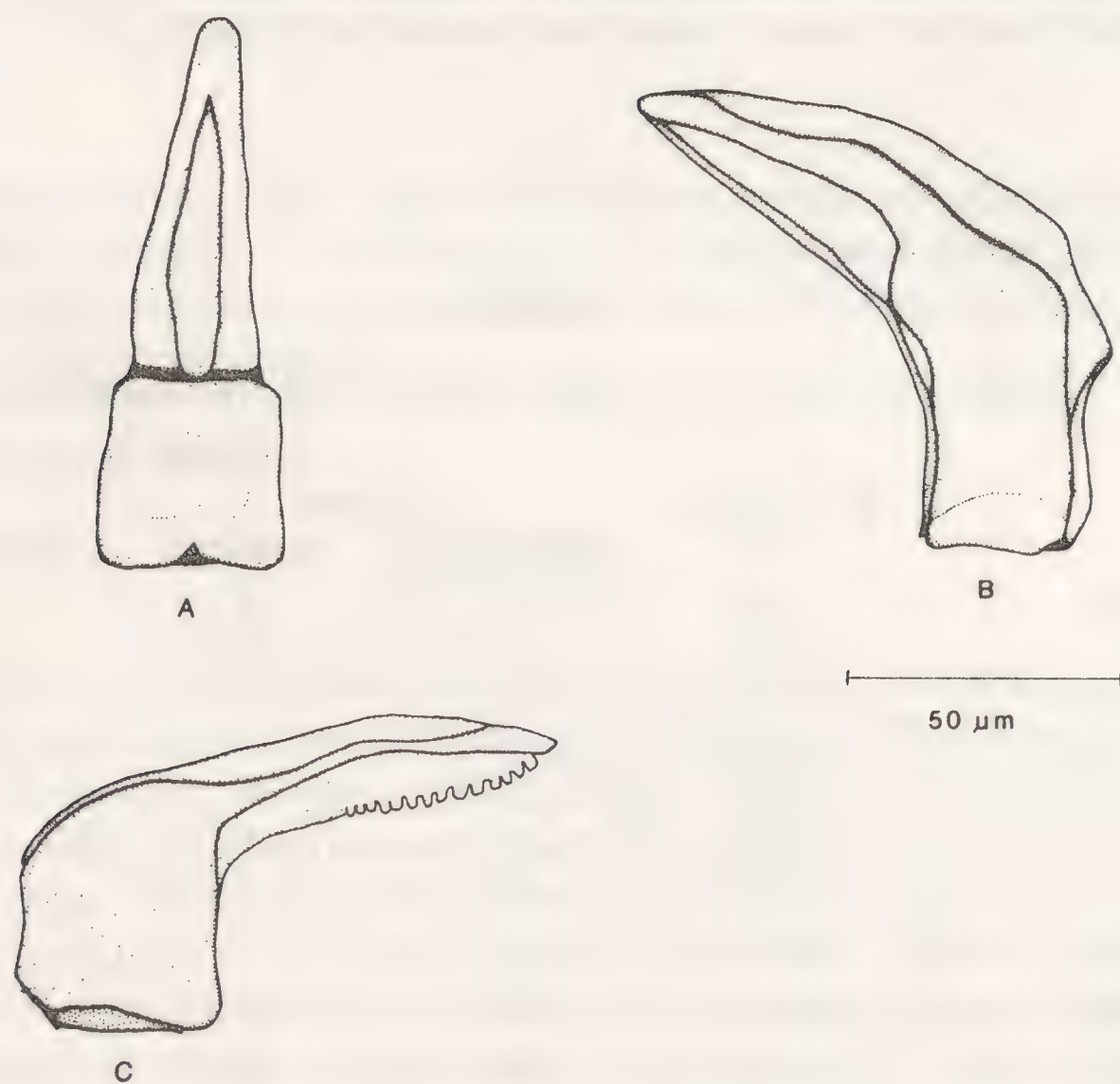


Fig. 4. Radular teeth of *Elysia serca*. A—frontal view of tooth from Banana River specimen. B—lateral view of same. C—lateral view of tooth from Indian River specimen. Camera lucida drawings.



1955) (Fig. 4C). As in the specimens from the Banana River, the pattern of dorsal veins in juvenile specimens was that of *E. clena*, and in adult animals, that of *E. serca*.

Table 2 summarizes vein patterns for 12 *Elysia serca*. As seen in Fig. 2, the branches of the dorsal veins are very distinct. The number of branches differs on the left and right sides of the animal, as mentioned by Marcus (1955, 1980). As the hindmost vein from one side (the left in Fig. 2) of the pericardium also branches to the other side of the dorsum, it may be difficult, especially in preserved (contracted) specimens, to see whether there is only one unpaired middorsal vein, or paired veins. These characters are supposed to distinguish *E. catulus* (unpaired, middorsal vein) from *E. serca* (paired veins) (Marcus 1980). However, *E. catulus* is generally melanistic (Marcus 1972b), whereas melanism is very rare in *E. serca*; we have seen one black animal in about 100 specimens.

Table 3 summarizes measurements of radular teeth of *Elysia serca*. The ratios of outer to inner cusp lengths for animals from the Indian River are much higher than those of animals from Key Largo, whereas the ratios of the animals from the Banana River overlap both the other populations. Table 4 lists the number of radular teeth in different populations. This also differs between populations, probably because differences in shape of the teeth permit different densities of teeth on the radular ribbon.

TABLE 3

Radular measurements of *Elysia serca* from different populations.

Population	Body length, mm	Length of leading tooth, $\mu$ m				Ratio of outer:inner length of cusp
		Total <sup>1</sup>	Base	Cusp outer <sup>2</sup>	inner <sup>3</sup>	
Indian River	4.29	120	36	117.6	67.2	1.75
	2.91	108	28.8	108	69.6	1.55
	2.05	67.2	19.2	62.4	36	1.73
Key Largo	3.19	98.8	26	88.4	62.4	1.42
	2.80	109.2	36.4	93.6	72.8	1.29
	2.34	114.4	46.8	98.8	72.8	1.36
Banana River	n.d.	n.d.	28.8	93.6	56.4	1.66
	n.d.	n.d.	28.8	96	72	1.33
	n.d.	n.d.	33.6	108	69.6	1.55

<sup>1</sup>Measured from tip of cusp to lower posterior edge of base. <sup>2</sup>Measured from tip of cusp to upper posterior edge of base. <sup>3</sup>Measured from tip of cusp to upper anterior edge of base. n.d.—Not determined.

TABLE 4

Number of radular teeth of *Elysia serca*.

Population	Number of teeth in ascending limb	Number of teeth in descending limb
Key Largo	10	18
	9	14
	9	13
	9	12
Indian River	5	18
	5	17
	6	18



Figs. 5A and B are cross-sections of *Elysia serca*. The large muscular pharynx (ph) occupies most of the head region. The ascus (as) lies on the right side of the pharynx. This is seen in *E. catulus* as well (Marcus 1972b, 1980), and this may be related to the seagrass-feeding habits of the two species (Clark 1975, present study).

**Feeding method:** When feeding on *Halodule wrightii* Ascherson, *Elysia serca* closely applied its mouth area to the leaf surface. Movements of the radula could not be seen, but the head made rocking movements, presumably corresponding to the movement of the radula, and cell sap visibly moved through the esophagus. *E. serca* did not move from one cell to the next in a longitudinal row, but moved in a zig-zag pattern from side to side, eating 5–10 horizontally adjacent cells, advanced a little, and then again moved horizontally to the other side. The animals were also observed while feeding on the leaf blades of *Halophila engelmanni* Ascherson. They penetrated both layers of cells and sucked cell sap from at least 5–6 adjacent cells at a time. Also, all animals observed began feeding at the distal tip of an *H. engelmanni* leaf blade and ate downwards towards the base, forming a band-shaped feeding track. *E. serca* also fed on *Thalassia testudinum* Banks ex König, but not on *Padina* sp., which was mentioned as its food by Marcus (1957), nor would it feed on *Syringodium filiforme* Kützinger, *Halimeda discoidea* Decaisne, or *Caulerpa sertularioides* (Gmelin) Howe.

In the animals feeding on *Halodule wrightii*, the material in the intestine (fecal material) was seen as a purple loop extending forward from the region of the heart, then bending back to end in the anus at the anterior margin of the right parapodium.

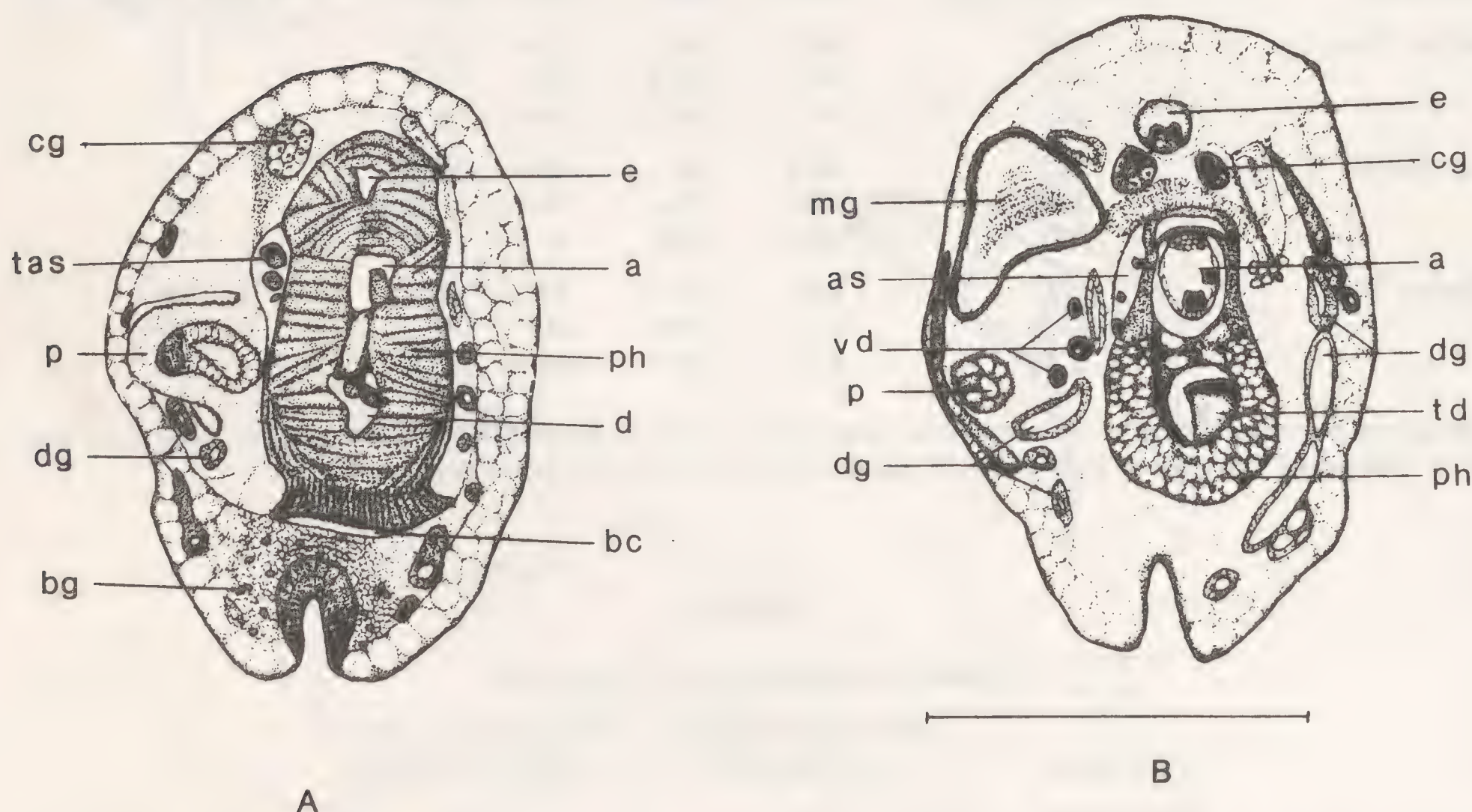


Fig. 5. Cross-sections of head region of *Elysia serca*. A—section through anterior part of pharynx. B—section through posterior part of pharynx. Camera lucida drawings.

Scale bar represents 0.5 mm. Legend: a—ascending limb of radula; as—ascus; bc—buccal cavity; bg—buccal gland cells; cg—cerebral ganglion; d—descending limb of radula; dg—digestive gland; e—esophagus; mg—mucus gland; p—penis; ph—pharyngeal musculature; tas—tooth in ascus; td—tooth in descending limb of radula; vd—vas deferens.



## DISCUSSION

The present study clearly shows that *Elysia serca* and *E. clena* are synonymous. *E. serca* Marcus 1955 has priority over *E. clena* Marcus and Marcus 1970. The two sets of characters generally used in separation of *E. serca* and *E. clena*, radular morphology and venation, are not reliable and show complete overlap in various geographical populations and with size of the animals. The reproductive anatomy, as given by Marcus (1955), Marcus and Marcus (1970), and Marcus (1980), also fails to provide differences of diagnostic value. Thus, the two species cannot be maintained, and *E. clena* should be considered an ecotypic variant of *E. serca*.

*Elysia serca* also shows great similarity to *E. catulus*, probably because both species feed on seagrasses (Clark 1975, present study). Both species have large heads, weakly developed parapodia, asymmetric dorsal veins, ascus on right side of pharynx, and teeth with cusps almost perpendicular to the tall bases (Marcus 1972b, 1980, present study). The colour of the two species differs, *E. catulus* being almost completely black (Marcus 1972b, Marcus 1980), and *E. serca* bright green with varying numbers of white dots, very rarely black (Marcus 1955, present study). Melanism varies ecotypically in other ascoglossans, as in *Ercolania fuscata* (Gould) (Clark pers. comm.) and *Limapontia depressa* Alder and Hancock (Gascoigne 1975). Because of the general similarity of *E. serca* and *E. catulus*, the two species may be synonymous, in which case *E. catulus* (Gould 1870) would be the senior synonym.

The record of *Elysia serca* feeding on *Ulva* (Hosoe 1956) needs reconfirmation by observation of actual feeding. Because *E. serca* feeds on flat food plants it is easily dislodged, and will often be found on other substrates than its actual food. This has also been observed in *E. catulus* (Clark pers. comm.), and may account for the report of *Sargassum* and *Padina* as food of *E. serca* (Marcus 1957).

The diets of *Elysia catulus* and *E. serca* differ, the former feeding exclusively on *Zostera marina* (Clark 1975) and the latter feeding on 3 other genera of seagrasses, *Halophila*, *Halodule*, and *Thalassia*. The geographical range of *Zostera marina* on the east coast of the U.S.A. does not overlap that of the other 3 genera of seagrasses (Hartog 1970). This may be the only reason for the difference in food spectra in *E. catulus* and *E. serca*. The peculiar shape of the radular teeth of *E. serca* and *E. catulus* is probably an adaptation to feeding on seagrasses. Individual epidermal cells of these plants are probably too small to yield a sufficient amount of energy relative to the amount of energy spent on piercing the cell wall. Hence, *E. serca* has teeth shaped to permit piercing of more than one cell at a time, and possibly *E. catulus* feeds in the same manner. Only one other species of ascoglossa, *Ercolania nigra* (Lemche), has been observed to empty more than one cell at a time (Rasmussen 1973).

The similarities in morphology may validate placement of *Elysia catulus* and *E. serca* in a separate subgenus different from *Elysia* sensu stricto. However, this should not be *Elysiella*, as proposed by Bergh (1886) for *E. catulus*, because the teeth of the type species, *Elysiella pusillus* Bergh, are different from those of *Elysia catulus* and *E. serca*, and also the position of the ascus differs (Bergh 1872, present study).

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# LIVING SPECIMENS OF *FUSINUS (SINISTRALIA)* *GALLAGHERI* SMYTHE & CHATFIELD 1981 FROM MASIRAH, OMAN

JUNE E. CHATFIELD\* and KATHLEEN R. SMYTHE†

(Accepted for publication 14 November 1981)

*Abstract:* Details of the habitat and of living animals of *Fusinus (Sinistralia) gallagheri* are given for a recently described species of sinistral whelk found on the shores of the island of Masirah in the Sultanate of Oman. An account is also given of some of the soft parts together with the radula and operculum.

## INTRODUCTION

*Fusinus (Sinistralia) gallagheri* Smythe & Chatfield 1981 was described from sixty-seven dead shells found in different localities along the east coast of Masirah. After the submission of that paper live specimens were collected on Masirah by one of the authors (K.R.S.) and by Dr. Donald T. Bosch of Muscat and his family. Observations in the field on the habitat and on living specimens, together with dissection of the animal for the radula, form the basis of the present paper. In 1980, when we wrote the description, we had anticipated that *F. gallagheri* might live offshore, but, although living populations probably extend into the sublittoral zone, the live specimens here described were found on the lower shore at an exceptionally low spring tide.

## OBSERVATIONS IN THE FIELD

During December 1980 one of the authors (K.R.S.) visited the island and collected on the shore in the company of Dr Bosch, who has over twenty-five years of experience of collecting shells on the coasts of Oman. Living specimens of *F. gallagheri* were found on 19 and 21 December during exceptionally low spring tides (0.4 m at 13.34 local time) between Ra's al Ya and Ra's al Jazirah, including the beach at Rassier, the type locality (map in Smythe and Chatfield 1981). Other beaches south of Ra's al Ya were explored, including Haql and Urf which had similar types of habitat, and dead, but no living, specimens were found. This negative result may well have been due to the less favourable state of the tide when these sites were visited. The habitat at these localities consisted of rocky reefs with sandy beach between; loose weedless rocks and sandy pools were distributed on the adjacent beaches. The whole of this east coast of Masirah is very exposed with a heavy surf.

*F. gallagheri* was collected under rocks or in crevices on the reef and only at the extreme low tide level. The rocks in this zone were exposed for less than two hours at low tide on

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these good springs and would not normally be uncovered at all during neaps. *F. gallagheri* was abundant in this position and was found living in all the rocky areas between Ra's al Ya and Ra's al Jazirah. It was not found on the single long stretch of sandy beach between these two headlands where living specimens of *Bullia rogersi* Smythe (Smythe and Chatfield 1981) were found on the same dates.

Predation of *F. gallagheri* by a naticid was postulated in our earlier paper from evidence of round bevelled holes in some of the shells: in December 1980 *Natica pulicaris* Philippi 1851 was very common in the sand between the rocks. On or under the same rocks as *F. gallagheri* and in some abundance were *Chiton lamyi* Dupuis 1917, *Diodora bombayana* Sowerby 1862 and *Fissurella townsendi* Melvill 1897.

## SHELL

Empty shells were described and illustrated in our earlier paper. The shell of *F. gallagheri* is a striking one, brown with white nodules, but those found alive in the field had the markings obscured by a variety of encrusting marine organisms. These encrustations included colonies of bryozoans, barnacles, coralline algae and a red alga, the last forming maroon patches.

## THE LIVING ANIMAL

Living animals were collected from Rassier and kept for some of the time in an aerated aquarium and some of the time in seawater in jars, depending on the facilities available. Several survived and were brought to England where they were kept alive until mid-January 1981. They did not prove to be very active at any time in captivity but the following observations were made: the sole of the foot and part of the lower side of the animal were crimson red in colour, the dorsal surface and short siphon were mahogany brown and the tentacles on the head were red, short and stubby but with slender elongated tips.

## OPERCULUM

The operculum closes the mouth of the shell when the animal withdraws. In *F. gallagheri* the operculum is an irregular oval shape with the width rather more than half of the length (Fig. 1). Unlike the opercula of many other marine prosobranchs, it is not flat but somewhat arched and twisted so that the outer surface is markedly convex although one edge curves upward giving a narrow concave area running alongside the columella of the shell. The outer face is mid-brown in colour, not glossy, and sculptured with somewhat irregular concentric growth ridges. The nucleus, in common with the opercula of other buccinids, is towards the apex, which is truncate.

Careful detachment of the operculum allows inspection of the inner surface. This is essentially concave and consists of two contrasting areas, each occupying about 50% of the surface. Towards the labial edge (next to the outer lip of the shell) is an oval area which is pale brown and with a matt surface, somewhat granular when examined under a microscope. This is the muscle scar where ends of branches of the columellar muscle are attached to the surface of the operculum by minute strands of tissue from the skin cells (microvilli). A single



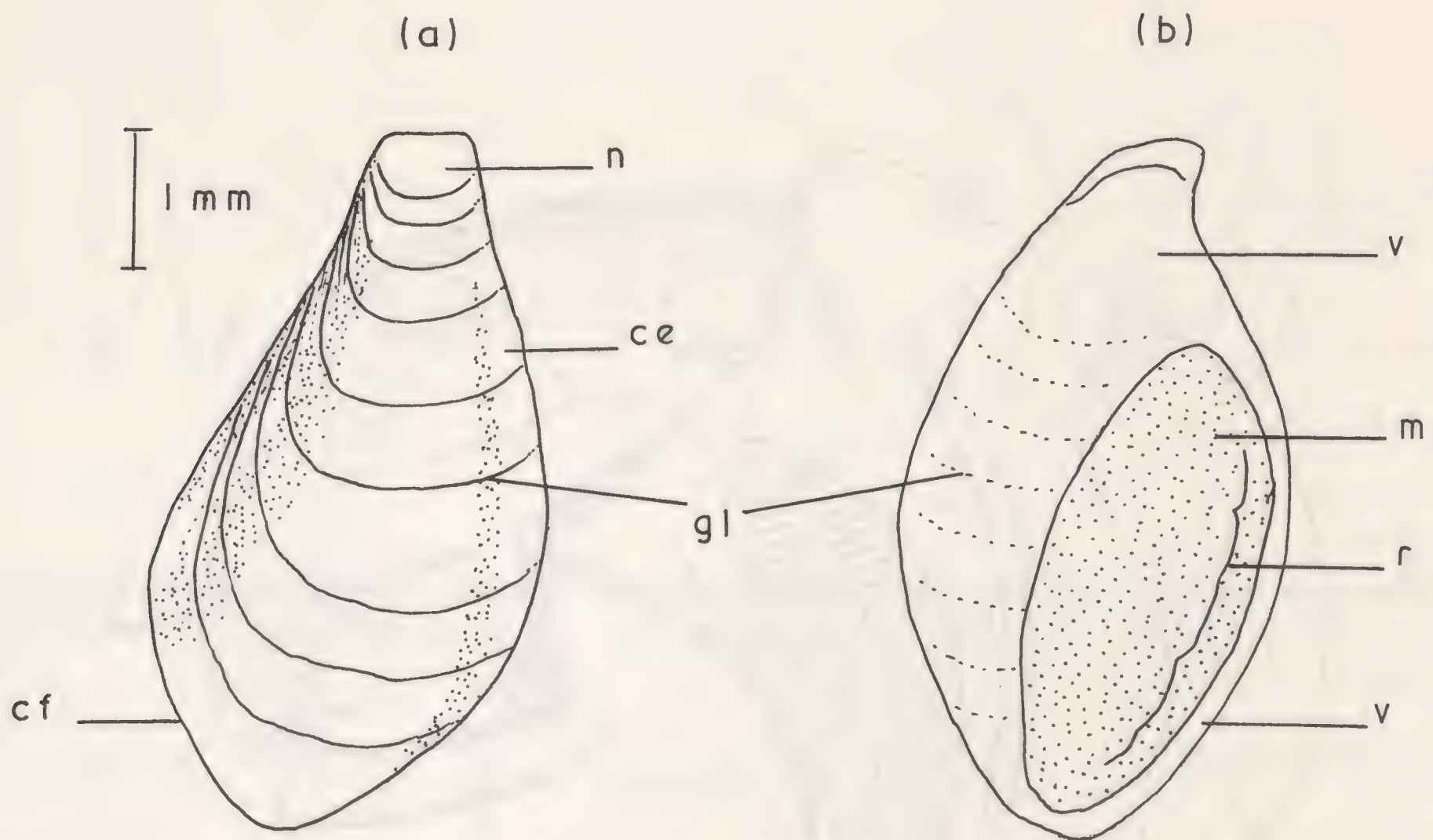


Fig. 1. operculum of *Fusinus (Sinistralia) gallagheri*. 1a, outer convex surface; 1b, inner concave surface. Key to labels: ce, concave edge; cf, convex flexure; gl, growth lines; ms, muscle scar; n, nucleus; r, ridge; v, varnish layer. This operculum came from a shell 20.52 mm  $\times$  11.00 mm.

smooth dark ridge is present towards the labial side of the muscle scar; there are many such ridges in other related genera (*Peristernia*, *Latirus*, *Fasciolaria* and *Pleuroploca*). The other half of the underside of the operculum contrasts markedly with the muscle scar area, being of a rich chestnut brown and highly glossy. This is the varnish layer referred to by Fretter and Graham (1962). The operculum of *F. gallagheri* is of a horny, rather than a calcareous, composition.

#### SOFT PARTS

The live animals collected were divided into three groups, some being kept alive, some preserved in 10% formalin, and some in 70% alcohol. External features visible when the animal is extracted from the shell (Fig. 2) include the head with snout, the contracted foot bearing the operculum, the mantle edge, and the thickened, pigmented area in the position of the contracted siphon. Through the thin skin of the roof of the mantle can be seen the ctenidium (gill) and opaque white osphradium (chemoreceptor or taste organ) which are on the right hand side instead of the left as in dextral molluscs.

#### RADULA

The radula of *F. gallagheri* is long (c. 6 mm), narrow (0.16 mm) and colourless. It consists of three teeth, comprising a central tooth or rachidian bearing three cusps, and a pair of broad lateral teeth each armed with six pointed cusps, and additionally a small cusp on the inner or median edge which probably articulates with the outer edge of the central tooth (Fig. 3).

In some of the radulae examined there was variation between the cusps on the two lateral teeth of the same row and also variation from one row to the next. In addition, newly formed teeth which had not yet been used had sharply pointed cusps whilst the functional teeth at the



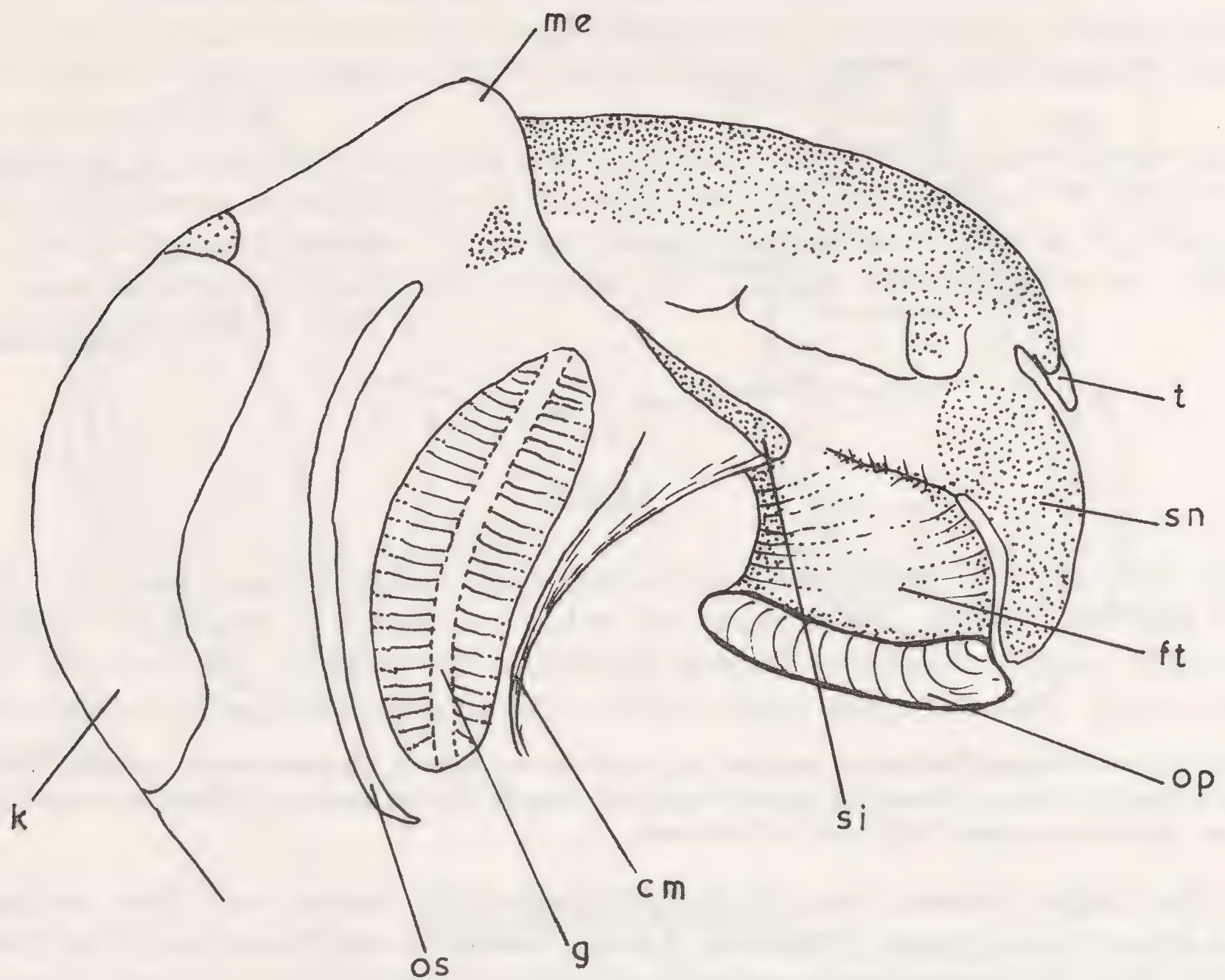


Fig. 2. *Fustinus (Sinistralia) gallagheri* removed from its shell to show the soft parts. Key: cm columellar muscle; ft foot; g, gill; k, kidney; me, mantle edge and entrance to mantle cavity; op, operculum; os, osphradium or chemoreceptor; si, siphon; sn, snout; t, tentacle.

mouth showed signs of wear, making the cusps rounded instead of pointed at the edge. The radula of *F. gallagheri* belongs to the Rachiglossan type, with a central rachidian and a broad lateral tooth on either side; this is typical of the superfamilies Muricacea and Buccinacea (Fretter and Graham 1962).

The detailed structure of the radula of *F. gallagheri* compares closely with those of other members of the genus *Fustinus* in the subfamily Fusininae. It differs from the fairly closely related genus of *Peristernia* (sub-family Fasciolariinae) in the shape of the central tooth which is pear-shaped in *Peristernia* but trapezoidal in *Fustinus gallagheri*, and also differs from other members of the Fasciolariinae (*Fasciolaria*, *Latirus*) in having comparatively narrower lateral teeth with fewer and less even cusps in the adult stage. *Fustinus gallagheri* has six main cusps on the lateral teeth compared with ten or more in *Fasciolaria*. Illustrations of the radulae in these tropical genera of Fasciolariidae are given in Barnard (1959). The pointed and curved cusps on the teeth of *Fustinus gallagheri* are almost certainly used to tear animal tissues for food, since, in common with other buccinids, this species is probably a scavenger feeding on soft-bodied invertebrates like marine worms.



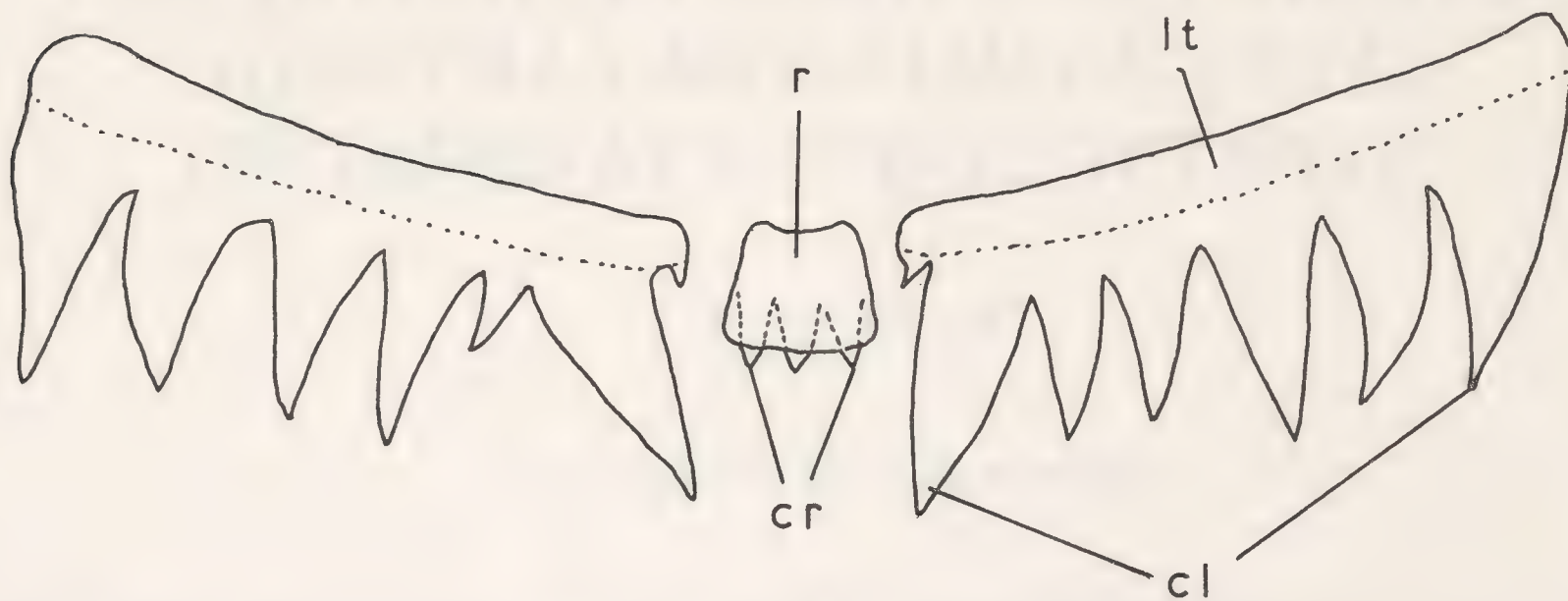


Fig. 3. Radula of *Fusinus (Sinistralia) gallagheri*; one row of teeth from the radula of the same specimen used for the operculum. Key: cl, cusps of lateral tooth; cr, cusps of rachidian or central tooth; r, rachidian.

### DISCUSSION

The shells of the subgenus *Sinistralia* are placed in the family Fascioliidae, the subfamily Fusininae and the genus *Fusinus*. They differ from the members of the related subfamily Fascioliinae (which includes *Latirus*, *Peristernia* and *Fasciolaria*) principally in the reduction of folds on the columella, the folds being markedly absent in *Fusinus*. Details of the radula serve to identify the genera but are not useful in separating the subfamilies. Although some members of the subgenus *Sinistralia* are taller and more slender than *F. (S.) gallagheri*, as a whole they do not have the extremely tall spire and long, straight siphonal canal that typifies most species of *Fusinus*. One other subgenus of *Fusinus* (*Aptyxis* Troschel, with a short siphonal canal) is similarly shorter and broader than the more typical examples of *Fusinus* (Keen 1971). Most species of *Fusinus s.l.*, which includes the taller shells of the genus, live on soft bottoms of mud, sand or silt, while the shorter examples of the genus like *Fusinus (Aptyxis) cinereus* (Reeve) from the Californian coast (Keen 1971) and *F. (S.) gallagheri* typically occur in rocky habitats and it is probable that other species of *Sinistralia* do likewise. A single live-collected but un-named specimen of *Sinistralia* which has been seen by one of the authors (J.E.C.) was also found on a reef.

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# THE JAMAICAN LAND SNAIL GENERA *GEOSCALA* AND *SIMPLICERVIX* (PULMONATA: UROCOPTIDAE)

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(Accepted for publication 14 November 1981)

*Abstract:* The Jamaican urocoptid genera *Geoscala* Pilsbry & Vanatta 1898 and *Simplicervix* Pilsbry 1903 are revised and their anatomy described for the first time. *Geoscala* has a shell with large white ribs, often split into two series above and below the periphery, and with 9–15 occurring on the penultimate whorl. Internally, the genitalia are completely separate from the right ocular retractor. Radula formula is 4:2:1:2:4; the central is weakly bilobed; the laterals enormous with elongate, symmetrical mesocones. *Simplicervix* has a shell with fine continuous ribs; 55–80 on the penultimate whorl. The right ocular retractor is attached to the vagina. Radula formula is 5:2:1:2:5; the central is weakly trilobed; the laterals proportionately broader and assymetrical. Both genera have small (5–11 mm) shells with an originally perforate apex which are decollate as adults and uncoil before the aperture; a globular spermatheca; a separate penial retractor muscle; both ocular retractors attached to the pharyngeal retractor; a radula with two enormous laterals and distinct marginals and are therefore assigned to the sub-family Apominae Paul 1982.

*G. seminuda* has deep sutures and an obsolete lower series of ribs, *G. robertsi* shallow sutures and both series of ribs, while *G. costulata* is smaller and has continuous ribs. *G. seminuda* and *G. robertsi* inhabit dry limestone forest along the south and north coasts, respectively. *G. costulata* and *S. inornata* occur in wet limestone forest of the central highlands. Neither *S. humilis* nor *S. simplex* has been rediscovered since their original description. *S. humilis* is illustrated for the first time.

## INTRODUCTION

Jamaica has one of the most diverse and interesting non-marine molluscan faunas of any region of comparable size in the world. Not only is it rich in species and varieties, but it includes forms such as the Urocoptidae, with distinctive shell shapes, the function of which is poorly understood. Furthermore, many species, or species complexes, show local variation which could be a treasure trove to ecologists and population geneticists. Yet, surprisingly, the Jamaican non-marine molluscs have received very little serious study. This is at least partly because of the lack of modern revisions of the various families, which makes it difficult to identify specimens. After a spate of species descriptions in the middle nineteenth century, very largely without illustration, most papers dealing with Jamaican non-marine molluscs have either been lists of species recorded on collecting trips (e.g. Gloyne 1872, 1875, Henderson 1894a–c, Pilsbry and Brown 1910, 1911, Baker 1934a–b, 1935a–d) or more general papers on the distribution of the Caribbean non-marine fauna (e.g. Bland 1861, Simpson 1894, Hunter 1955).

This situation remained unchanged until Johnson and Boss (1972) and Jacobson and Boss (1973) selected and figured type specimens of nearly all of C. B. Adams' species and varieties of Jamaican non-marine molluscs; a mammoth task involving publishing photographs of nearly 300 shells. Although a few of Adams' types could not be located, these papers mark a great step forward and provide a basis for the assessment of the many taxa described by Adams. The Hon. Edward Chitty (1804–1863) and Professor C. B. Adams (1814–1853) described more Jamaican molluscs than all other authors put together. Chitty

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held several legal posts in Jamaica, while Adams was Professor of Zoology and Astronomy at Amherst College at the time of his premature death in 1853. Prof. Adams met Chitty in Jamaica on his first visit in 1844, became a firm friend and stimulated the latter's interest in Jamaican molluscs. Chitty collected material and sent it to Adams for description. Adams and Chitty planned a monograph of Jamaican non-marine molluscs, but after Adams' death in St. Thomas in 1853, Chitty abandoned the project, although he did continue Adams' 'Contributions to Conchology' with a thirteenth part and he published three more papers on Jamaican non-marine molluscs (Chitty 1853, 1854, 1857a-b). As a result, both authors published preliminary descriptions only and just two of their numerous taxa were ever figured (*Urocoptis megacheila* and *U. amethystina*). Adams made an extensive collection of Jamaican molluscs which remained at Amherst College after his death until it was transferred to the Museum of Comparative Zoology at Harvard (MCZ) in 1942, where it is still. It was from this collection that Johnson and Boss (1972) and Jacobson and Boss (1973) selected and figured type specimens of Adams' freshwater and terrestrial species, respectively. Clench and Turner (1950) figured type specimens of eight of Chitty's species, including that of *U. megacheila*, one of the two species Chitty (1853) originally figured himself.

Chitty also made a very extensive collection of Jamaican shells which initially resided in the rooms of the Royal Society of Arts of Jamaica, of which Chitty was an active member. At about the time of Chitty's departure from the island the society collapsed and Chitty's collection was stored. It was transferred to the storeroom by patients of the lunatic asylum at Rae Town, suffered greatly during its period of storage and eventually came into the hands of the Jamaica Institute, very much the worse for wear, sometime before 1899 (Vendryes 1899, p. 592 gives a more detailed account of the history of Chitty's Jamaican collection up to that time). As if that were not enough, the Jamaica Institute was demolished by an earthquake on 14 January 1907, and what was left of Chitty's Jamaican collection was almost completely destroyed. Longstaff (1912) gives an account of the earthquake.

Fortunately, before Chitty left Jamaica, Adams selected representative examples of each form to be deposited in the British Museum, Natural History (BMNH), in London. Adams made a catalogue of the material he removed from Chitty's Jamaican collection, which presumably remained with the main collection in Jamaica. Chitty copied Adams catalogue and it is Chitty's copy which accompanies his first collection in the BMNH, which was catalogued by the BMNH in 1854, has BMNH catalogue numbers starting 54 and usually Chitty/Adams catalogue numbers as well. Most of this collection is still kept separate from the main BMNH collections, although now stored in glass tubes not mounted on tablets. Only the Urocoptidae have been incorporated into the main collection. I have used Chitty's catalogue to identify his handwriting on labels of urocoptids in the main collection.

Chitty also brought more material back with him when he left Jamaica, which was catalogued in 1857, has BMNH catalogue numbers beginning 57 and does not have Chitty/Adams catalogue numbers. Chitty's second collection does not have the same authority for Adams' taxa, since it was identified by Chitty not Adams himself, however, it is still very important, as in the case of *Simplicervix humilis* (Adams) and it contains type material of Chitty's species and varieties. I propose to refer to this as Chitty's second BMNH collection. Both Chitty collections have also survived well.

It may seem unnecessary to refer to Chitty's two collections when so many of Adams' types have been selected and figured. However, Jacobson and Boss (1973, pp. 309-310) list 27 terrestrial, 38 marine and 3 freshwater taxa of which they were unable to locate any type material. Chitty's first BMNH collection is the next most obvious place to look since it contains specimens authenticated by Adams. Thus the combination of the Adams collection at Harvard and Chitty's two collections in London should enable a thorough revision of almost all species and varieties described by Adams and Chitty. Urocoptid species described by European authors before Adams' time may or may not have traceable types, while those



described by Pilsbry (1902–1903b), Pilsbry and Brown (1910, 1911) and H. B. Baker (1935b–c) are in the Academy of Natural Sciences, Philadelphia (ANSP). Altogether the position as regards types of Jamaican non-marine molluscs is very satisfactory considering that 125 years have passed since most of them were described.

Normally the first reviser should select type specimens and localities where this has not already been done. Jacobson and Boss (1973) republished *without revision* the original descriptions of all C. B. Adams' land snails and selected and figured type specimens where shells could be found in Adams' collection. Selection of types without revision of the taxa involved is a hazardous process and in one or two cases the results have been rather unfortunate. However, the illustration of Adams' many taxa is probably the single most important contribution this century to the study of Jamaican molluscs and thorough revision of them all is a lifetime's work.

Jacobson and Boss (1973) did not select type localities, although they did publish any locality data (other than just 'Jamaica') which they found on original labels or in Adams' manuscript catalogue. They also published a map (1973, map 1, p. 313) drawn by Adams himself showing the localities he visited. They further suggested (1973, p. 309) that in selecting type localities, future workers would be advised to choose them from the areas Adams is known to have visited. However, I do not agree that such a restriction is justified on the available evidence. In his original descriptions Adams rarely indicates the source of his shells. It is known that Chitty provided him with many specimens and of the six species revised in this paper, type material has accompanying labels including the following information:— the lectotype and/or paralectotypes of *G. seminuda* and *S. inornata* were collected by Chitty; all types (four examples) of *G. robertsi* are from the Bland collection with no indication as to who collected them (merely that Bland received them from Adams); Adams collected type material of *G. costulata*; there is no indication as to who collected the solitary known specimen of *S. simplex* and Adams collection lacks any specimens of *S. humilis*. Since Chitty's second BMNH collection contains five examples of the last species, it is likely that Chitty collected the original example(s) as well. From this it hardly seems likely that specimens upon which Adams' original descriptions were based came only from the areas visited by Adams himself. In selecting type localities I have tried to discover whence the original specimens came. Failing this, I have chosen either a locality from which Chitty collected or one where the species is common and which lies well within its known range. Localities are indicated by place name, parish and the coordinates of the Jamaican grid (Fig. 1) with E-W coordinates given first. Details are taken from the 1:50,000 sheets. Four figure co-ordinates, e.g. 6037 for Port Royal, Kingston, define a square approximately 3 km by 3 km.

In this paper I am revising the Jamaican species which Pilsbry (1930b) attributed to the subgenera *Brachypodella* (*Geoscala*) and *B. (Simplicervix)*. Species of these two genera have had little nomenclatural history and are generally correctly identified in collections. The Urocoptidae as a whole are fascinating animals with unusual shell morphology. I hope to discuss the function of shell shape and decollation in the Jamaican forms in a future paper, while the comparative anatomy, morphology and systematics of Jamaican Urocoptidae have been described elsewhere (Paul, 1982).

## SYSTEMATIC DESCRIPTIONS

### Family Urocoptidae Pilsbry & Vanatta 1898

*Definition:* Shells cylindrical, fusiform or conical in adults, frequently decollate, composed of many narrow whorls, the last sometimes uncoiled. Aperture small, circular or squarish,



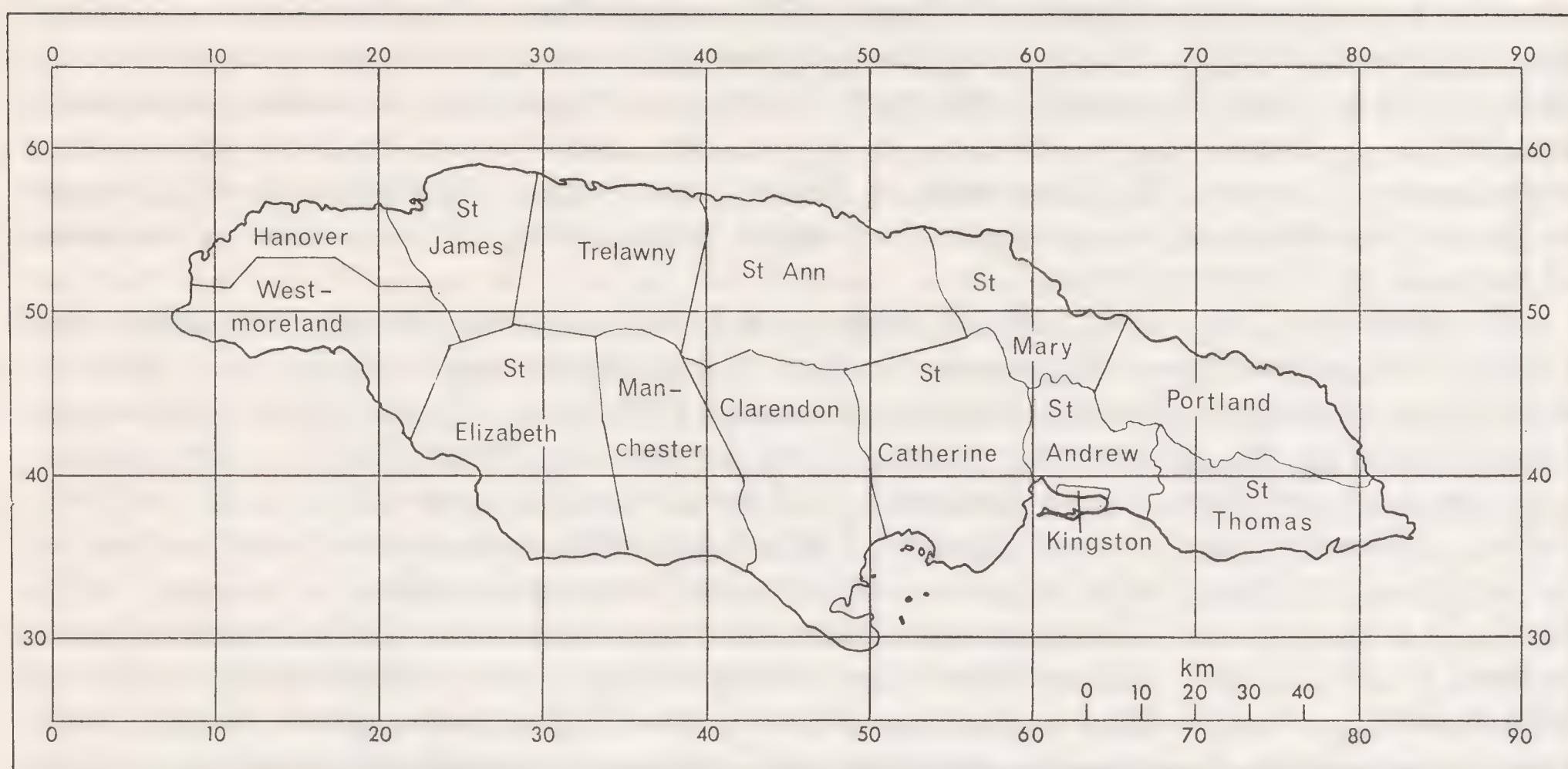


Fig. 1. Outline map of Jamaica to show Jamaican grid and parishes.

without barriers or constrictions; peristome generally entire, reflected and sometimes thickened. Axis hollow or solid, simple or variously twisted and thickened.

Body with small foot with simple sole, united by a long pedicel to the main visceral mass. Jaw pleated, striate or smooth. Radula often very long with relatively few teeth per row. Lung long and narrow, with long pulmonary vein, but otherwise weak venation. Kidney narrow, wedge-shaped, about as long as the pericardium. Genitalia hermaphrodite. Spermatheca at the end of a long duct. Lower genitalia simple, without accessory structures such as mucous glands. (Modified from Pilsbry 1904, p. vii.)

*Distribution:* Caribbean Islands and adjacent mainland areas from Florida through the Gulf Coast States and Central America to the north coast of South America.

*Remarks:* Until recently the Urocoptidae were divided into three subfamilies; the Eucalodiinae, Microceraminae and Urocoptinae, largely on the basis of radular characters (see Zilch 1960, pp. 522–543). However, Jaume & de la Torre (1976) have recognized six subfamilies among the Cuban urocoptids, but their scheme does not work for Jamaican genera which have little in common with the Cuban fauna. Jamaican genera fall convincingly into three subfamilies (Paul 1982). Both genera considered here belong in the Apominae which is a group with distinctive shell morphology and anatomy (see definition below). Too little is yet known of the anatomy of similar forms in Cuba or elsewhere, but the Jamaican apomines can be distinguished from all Cuban shells by their peculiar perforate apex (Plate 2, figs. 4–11).



## Subfamily Apominae Paul, 1982

*Definition:* Urocoptids characterized by an elongate, decollate, shell with many whorls, that usually uncoils a little before forming the aperture and has a perforate apex; with a very long and thin radula with narrow weakly lobed centrals flanked on either side by a pair of relatively enormous laterals with weak or absent ectocones and four to eight small bifid marginals. Genital anatomy is characterized by a globular spermatheca and the retention of a separate penial retractor muscle. Both ocular retractors are associated with the pharyngeal retractor and have multiple insertions anteriorly (see Paul 1982 for further details).

*Remarks:* As defined above the subfamily includes only the Jamaican genera *Apoma* Beck 1837, *Mychostoma* Albers 1850, *Geoscala* Pilsbry & Vanatta 1898 and *Simplicervix* Pilsbry 1903. The latter pair are characterized by small shells and are oviparous as far as is known. The former pair are larger and at least some species are known to be ovoviviparous. They will form the subject of a separate paper. A perforate apex is found in a number of other non-Jamaican species of *Brachypodella* s.l. from the eastern Greater Antilles, the Lesser Antilles and Central America, but the anatomy of these species remains unknown. For the present they are best left unassigned to a subfamily, although some of them will likely prove to belong with the Jamaican apomines.

*Geoscala* and *Simplicervix* have three species each, although two forms of *Simplicervix* have not been seen since they were first described in the mid nineteenth century. *Geoscala* has a distinctive shell with prominent vertical lamellae, while *Simplicervix* has closely spaced fine sharp-crested ribs (Plates 1 and 2). As with virtually all Jamaican urocoptids, they are confined to limestone areas and these two genera live on rocks.

Genus *Geoscala* Pilsbry & Vanatta 1898

*Type species:* *Cylindrella seminuda* Adams 1845, by original designation (Pilsbry & Vanatta 1898, p. 279).

*Definition:* A genus of Apominae with small, decollate, dextral shells. 6–10 whorls remain in the adults which are 6–10 mm high. The last whorl uncoils slightly and bears two distinct keels. All post nepionic whorls are striate and lower whorls are ornamented with prominent, vertical, white ribs which sometimes break up into two series and tend to impart a square outline to the whorls. The aperture is very slightly expanded, the peristome broadly reflected all round to form an aperture plane which is usually inclined at a small angle to the axis of coiling. The apex is characteristically perforate. Internally, the columella is simple and not thickened.

The body is pale, almost totally unpigmented, but with occasional specks or streaks of darker colour on the posterior dorsal surface. When fully extended the body is short,  $2\frac{1}{2}$ –3 mm long by  $1\frac{1}{2}$  mm maximum width, tall and steep sided with the posterior sloping gently and pointed. The ocular tentacles are short, about 1 mm when fully extended, with a black eye spot at the tip but otherwise unpigmented. The lower tentacles are entirely absent. The foot is shaped like the plan view of a ship, only with the posterior end pointed, and is wrinkled with transverse folds. It lacks a foot fringe, is undivided and parallel sided anteriorly. When crawling, at most two muscular contractions occur in the sole, the posterior one starting as the anterior one reaches the front. In juveniles and smaller examples only one contraction can ever be observed. In crawling the body extends forward about twice the length of the aperture and then the shell is dragged forwards by a major muscular contraction. Normal adult locomotion involves this shell dragging, but juveniles can and do raise the shell entirely off the substrate for protracted periods. The apical four whorls of the body appear dark due to the digestive gland; the lower whorls are pale but bear occasional darkly pigmented vertical streaks which in outline and spacing resemble the white vertical ribs on the shells. The lung extends for four whorls when the shell is fully occupied by the body, but the animal can



contract well back into the shell. As might be expected, this contraction is achieved quickly in one swift motion; the return slowly in a series of short pulses. The lower body occupies less than one whorl when retracted into the shell.

Internally, *Geoscala* is characterized by a penis which is longer, but thinner than the vagina and has a separate retractor muscle which inserts somewhere on the inner side of the coiled prostate; an extremely short free oviduct which is fatter than the basal spermatheca duct; a small globular spermatheca and a right ocular retractor which is not in any way connected to the genitalia. The radula is very long and thin (length/width=25–35) with a formula of 4:2:1:2:4×70–100. The central tooth is smoothly rounded, weakly bilobed and 8–15 µm wide. The two adjacent laterals have enormous smooth mesocones shaped like the sole of a shoe and with smooth round scraping surfaces. They are 25–30 µm wide, the inner entirely lacks an ectocone, the outer has a vestigial ectocone. The marginals are small and bear ectocones that are almost as large as the mesocones and aligned with them. The laterals are arranged in a V-shaped pattern, but the marginals are more or less transverse to the length of the radula. Thus the whole row of teeth has a V-shaped profile. The columellar muscle gives rise to one additional retractor which then splits almost immediately into three, the left and right ocular retractors on appropriate sides and the pharyngeal retractor in the centre. Both ocular retractors divide near the buccal mass, sending a pedal branch to the foot floor beneath the buccal mass, an ocular branch to each ocular tentacle and an anterior branch to the front of the buccal mass.

*Ecology:* Species of *Geoscala* are confined to limestone areas where they live on rock outcrops. They can often be found crawling in, or attached to the sides of, solution hollows and they tend not to occur where thick leaf litter or soil cover the underlying rock. Baker (1935d, p. 58) records *G. seminuda* as a weak climber, but the only specimens I have seen above ground level were in honeycombed limestone outcrops. *G. seminuda* is typical of dry limestone forest (see Asprey & Robbins 1953 for definitions of Jamaican vegetation types) along the southern coastal strip, but penetrates inland where rainfall remains fairly low, notably around St. Thomas in ye Vale. *G. robertsi* is confined to the narrow, dry northern coastal strip, while *G. costulata* occurs in wet limestone forest in the central and western interior of Jamaica.

#### Key to the species of *Geoscala*

- |   |                     |
|---|---------------------|
| 1. Shell very small (5½–6½ mm), ribs entire, whorls rounded                 | <i>G. costulata</i> |
| Shell larger (7–10 mm), ribs in two series, whorls squarish                 | 2                   |
| 2. Suture extremely deep, shell sometimes pagodiform in the last two whorls | <i>G. seminuda</i>  |
| Suture shallow  | <i>G. robertsi</i>  |

In *Geoscala* the most useful characters on which to identify the shells are size, depth of suture and the ribs or lamellae. *G. costulata* (Plate 1, figs. 4–6) is small, with moderately deep sutures, more rounded whorls and more continuous ribs (Plate 2, fig. 11). *G. robertsi* is larger and has much more shallow sutures (Plate 1, figs. 10–12) with squarish or flattened whorls and usually two almost equally developed series of ribs above and below the periphery (Plate 2, fig. 12). *G. seminuda* is slightly smaller than *G. robertsi*, has deep to extremely deep sutures, squarish or undercut triangular whorls (Plate 1, figs. 1–3) and two series of ribs, the lower of which may become obsolescent or disappear entirely (Plate 2, fig. 10).

*Geoscala seminuda* (C. B. Adams 1845) Plate 1, figs. 1–3; Plate 2, figs. 4, 8, 12; Plate 3, figs. 4–6; Plate 4, figs. 1–3; text-figures 2–5.

*Cylindrella seminuda* C. B. Adams 1845 (January): 14. Pfeiffer (in Philippi) 1845 (October): 51,



pl. 2\*, fig. 16. Pfeiffer 1848: 380. Bland 1861: 356. Bland & Binney 1872: 184. Gloyne 1875: 122. Sowerby 1875: pl. 5, fig. 46. Henderson 1894b: 20. Jacobson & Boss 1973: 418, pl. 61, fig. 17.

*Urocoptis (Brachypodella) seminuda* (C. B. Adams)—H. & A. Adams 1855: 177.

*Cylindrella (Mychostoma) seminuda* C. B. Adams—Pfeiffer 1860: 46, 1861: pl. 5, fig. 46.

*Cylindrella minuda* (sic)—Rush 1891: 69

*Brachypodella (Geoscala) seminuda* (C. B. Adams)—Pilsbry & Vanatta 1898: 279. Pilsbry 1903b: 92, pl. 5, figs. 41–2, 44. Thiele 1931: 675, fig. 731. Baker 1935d: 58. Zilch 1960: 542, fig. 1895.

*Mychostoma seminuda* (C. B. Adams)—Vendryes 1899: 599.

*Brachypodella seminuda* (C. B. Adams)—Pilsbry & Brown 1911: 579.

*Types*: Lectotype MCZ 155909 (Plate 1, figs. 1–3), by designation of Jacobson & Boss 1973, pl. 61, fig. 17; paralectotypes MCZ 275694 (2 examples ex Chitty); MCZ 155910 (48 examples); and four other lots.

*Type locality*: Jacobson & Boss (1973, p. 418) indicate that Rock Spring's, St. Mary (Jamaican co-ordinates 5749) is given as a locality in either Adams' manuscript catalogue of shells or an original label. If the latter, I did not see it when I examined the collection in August 1977. The lectotype has a label that indicates it came from 'St. David's, Jamaica'. Specimens in Chitty's BMNH collection are labelled 'Easington, St. Thomas' (Jamaican co-ordinates 6937). Modern maps mark a 'District of Upper St. David' and a 'District of Lower St. David' to the north and east of Yallahs, St. Thomas, which lie between E-W co-ordinates 70 and 73 and N-S co-ordinates 35 and 40. Easington is just on the western edge of the District of Lower St. David and hence seems an appropriate type locality.

#### *Description.*

a. Shell: cylindrical to fusiform, small, 7–8 mm when decollate, up to 10 mm complete, moderately elongate (height/diameter about 3), normally decollate and with the last quarter whorl uncoiled and free. Surface of mature shell ornamented with prominent, opaque white ribs on the top and bottom of each whorl, but only weakly developed or entirely absent on the periphery. The lower series of ribs is the weaker and is often obsolescent or absent. There are 21 ribs on the penultimate whorl of the lectotype, usually about 20–22. Shells are translucent white when fresh, becoming opaque white with age.

There are 6–9 whorls in the adult shell, 13 in a complete shell (BMNH 57.12.1.523, Chitty coll., Fig. 3d), but as many as 10–11 whorls may be lost (MCZ). Outline of whorls is squarish when both series of ribs are developed, becoming triangular in the lower whorls if the lower ribs are absent and the suture is extremely deep (cf Figs. 2a and c). The uncoiled part of the last whorl has two prominent keels, the upper one about twice as broad as the lower (Figs. 2b, 3d).

The protoconch is very finely striate, high-sided initially and perforate (Plate 2, figs. 4, 8). The nepionic shell consists of three whorls. Three to nine juvenile whorls follow. Initially they have rounded outlines, but they become more square as the fine continuous striae give way to the two series of short ribs.

The aperture is entire (Fig. 2c), free in mature adult shells, and roughly diamond shaped. The two keels on the free portion produce the angles in the outline of the aperture. The lip is reflected at almost right angles to the neck all round. The aperture is not expanded significantly and the lip scarcely thickened at all. The reflected part of the lip is almost exactly planar, wider anteriorly and on the palatal lip. The plane of the aperture lies at between 13 and 22½° to the axis (Fig. 3a–b), but occasionally it may reach as much as 33° (Fig. 3c).

[\* *Cylindrella* plate 2=pl. IV of part X of Philippi's *Abbildungen*. Non *Cylindrella seminuda* Weinland 1880, p. 358, from Haiti.]



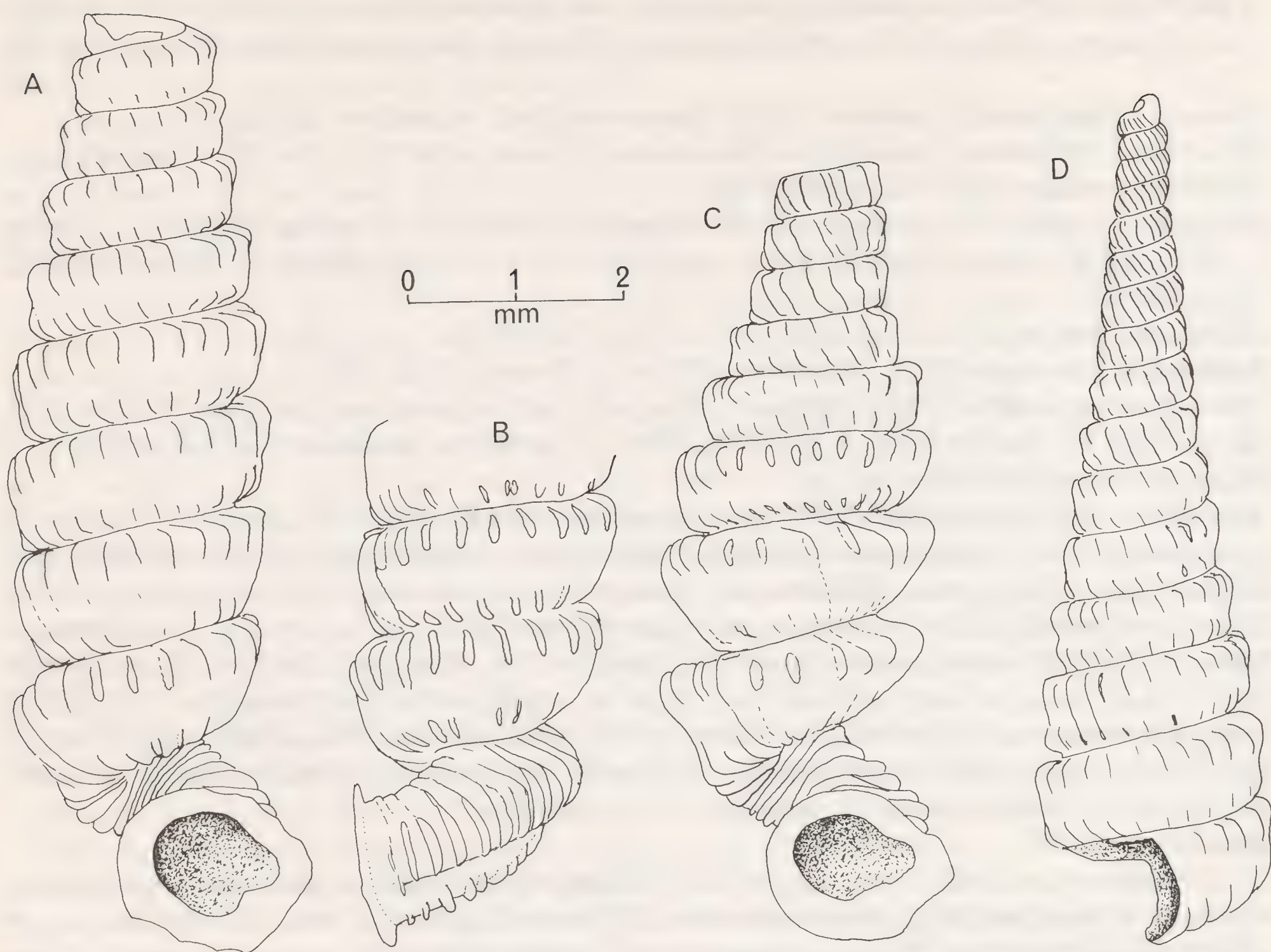


Fig. 2. Camera lucida drawings of shells of *Geoscala seminuda* (C. B. Adams). A-B, lectotype MCZ 155909, apertural and lateral views. C. paralectotype MCZ 155910a, an example of the variety with deeply undercut lower whorls. D, Paralectotype MCZ 155910b, a juvenile shell.

The periostracum (Plate 3, figs. 4–6) is very finely pitted. Internally the columella is simple and not thickened even in adult shells.

b. Anatomy (Fig. 4): As for the genus. The penis seems to be proportionately larger in *G. seminuda* than in the other two species, but how constant the difference is remains to be confirmed. The radula is extremely long for the body size (5.5–5.8 mm) and very thin (about 0.2 mm across). There are 90+ rows of teeth arranged 4:2:1:2:4. The central is weakly bilobed, 15  $\mu$ m wide and has rounded edges. The laterals are elongate and smoothly rounded, and 30  $\mu$ m wide (plate 4, figs. 1–3). The outer lateral has a vestigial ectocone in line with the marginal row. Marginals have small rounded meso- and ectocones, except the outermost one. The jaw is very thin, arched and pleated with about 20 folds on either side. As with all Jamaican urocoptids, as far as is known, the folds converge towards the midline. *Ecology*: *G. seminuda* extends from dry limestone forest into the moderately wet foothills of the central ranges in Jamaica. It is generally ground dwelling on limestone outcrops and can tolerate considerable drought.

*Variation*: Adult, decollate shells of *G. seminuda* range from 7.0–8.8 mm high (Table 1) and from 2.3–2.6 mm diameter. Occasional examples may remain complete and reach 10½ mm high. The number of ribs (upper series) on the penultimate whorl does not vary greatly, 20–25 is the usual number. The development of the lower series and the depth of the suture do vary considerably. In the lectotype the lower ribs are quite obvious and the last couple of whorls are not markedly undercut (Fig. 2a). In other examples the lower ribs are absent and



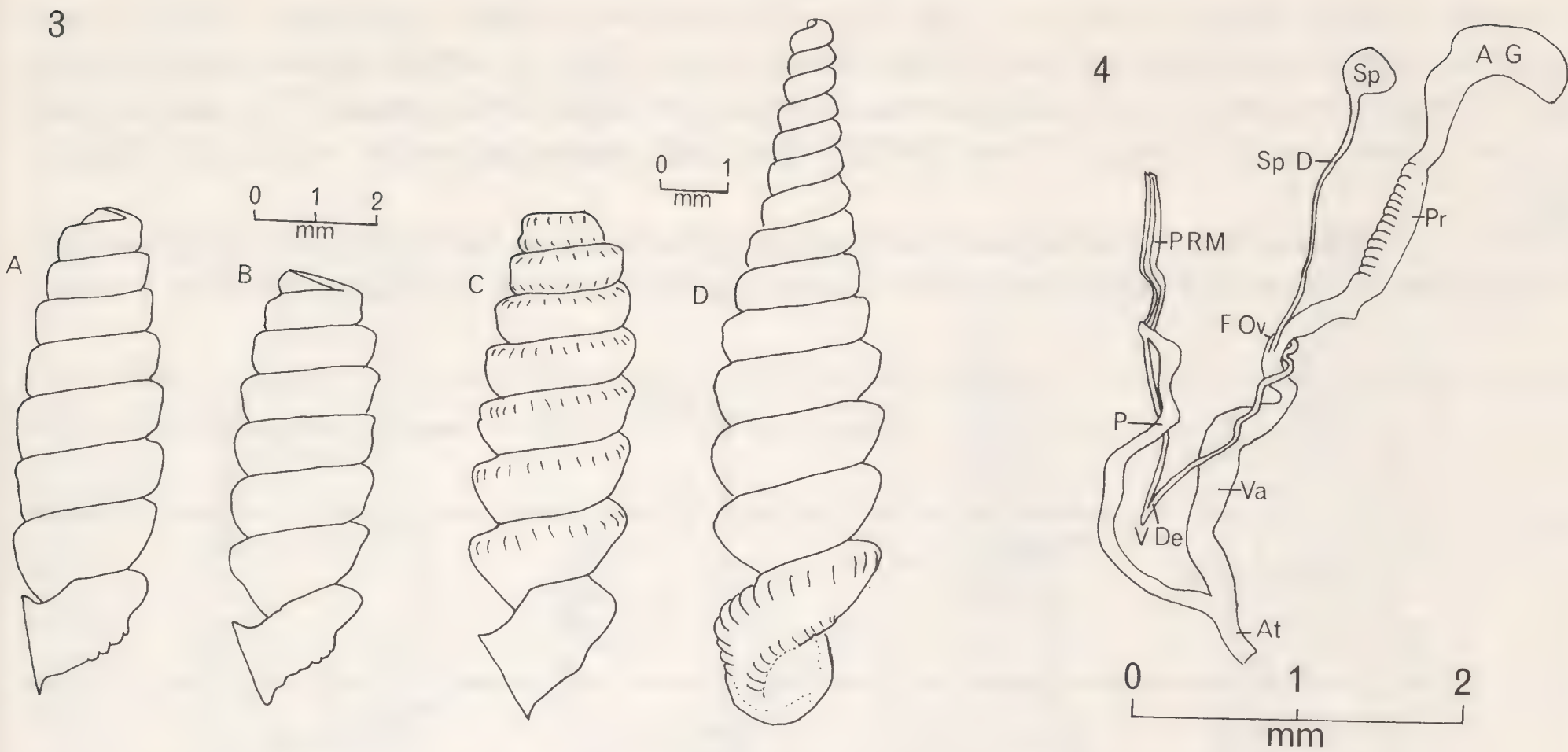


Fig. 3. Camera lucida drawings of shells of *Geoscala seminuda* (C. B. Adams) to show variation in  $\alpha$ , the angle between the aperture plane and the shell axis (A-C), and the two keels on the neck of the shell (D). A, C. P. coll., nr Santa Maria House, Red Hills, St. Catherine,  $\alpha=13^\circ$ ; B, B. Coles coll., Portland Ridge, Clarendon,  $\alpha=22\frac{1}{2}^\circ$ ; C, BMNH 53.1.29.11 (no locality),  $\alpha=34^\circ$ ; D, 2nd Chitty coll., BMNH 57.12.1.523a (no locality), a complete shell.

Fig. 4. Camera lucida drawing of the distal genital anatomy of *Geoscala seminuda* (C. B. Adams), nr Rectory, Manchester. AG albumen gland, At atrium, F Ov free oviduct, P penis, PRM penial retractor muscle, Pr prostate, Sp spermatheca, Sp D spermatheca duct, Va vagina, V De vas deferens. Penial retractor separated from prostate for clarity.

TABLE 1

Measurements in *Geoscala seminuda* (C. B. Adams)

Specimen	Height (mm)	Diameter (mm)	Whorls <sup>1</sup>	Ribs <sup>2</sup>	$\alpha^3$
Lectotype MCZ 155909	8.8	2.5	$8\frac{3}{4}$	21	—
Paralectotype MCZ 155910a	7.3	2.6	$8\frac{1}{4}$	—	—
C. Paul coll. nr Santa Maria House, St. Catherine	7.8	2.3	8	25	$18^\circ$
C. Paul coll. nr Santa Maria House, St. Catherine	7.7	2.4	7	23	$17^\circ$
C. Paul coll. nr Santa Maria House, St. Catherine	8.1	2.4	$7\frac{3}{4}$	23	$13^\circ$
C. Paul coll. nr Santa Maria House, St. Catherine	7.7	2.4	$7\frac{1}{2}$	25	$20^\circ$
B. Coles coll. Portland Ridge, Clarendon	7.2	2.35	$6\frac{1}{4}$	24	$22\frac{1}{2}^\circ$
B. Coles coll. Portland Ridge, Clarendon	7.8	2.4	7	23	$21\frac{1}{2}^\circ$
B. Coles coll. Portland Ridge, Clarendon	7.0	2.4	$6\frac{1}{4}$	24	$16^\circ$
1st Chitty coll. BMNH 54.4.19.354	8.3	2.4	$8\frac{1}{4}$	20	$18^\circ$
2nd Chitty coll. BMNH 57.12.1.523	10.5*	2.6	13*	—	—
BMNH 53.1.29.11	7.8	2.4	$7\frac{1}{4}$	22	$33\frac{1}{2}^\circ$

<sup>1</sup>Number of whorls remaining in adult shell. <sup>2</sup>Number of ribs on the penultimate whorl. <sup>3</sup>Angle between the aperture plane and the axis of the shell.  $\alpha$  was measured by making a camera lucida drawing of the shell orientated with the aperture perpendicular to the viewer and determining the axis by connecting the midpoints of the topmost and lowest complete suture and then measuring the angle between this axis and the line of the aperture plane. \* This shell complete.



the basal whorls deeply undercut (Fig. 2c). The undercut form apparently occurs most frequently in the south and west of the distribution area (Fig. 5), which agrees with the idea that the lectotype came from Easington near the eastern limit of the species. The angle of the aperture plane usually ranges from  $13\text{--}22\frac{1}{2}^\circ$ , but odd examples occur with much higher angles.

*Remarks:* *G. seminuda* is a common and distinctive species which can easily be recognized by the poor development of the lower series of ribs and by its deep to extremely deep suture.

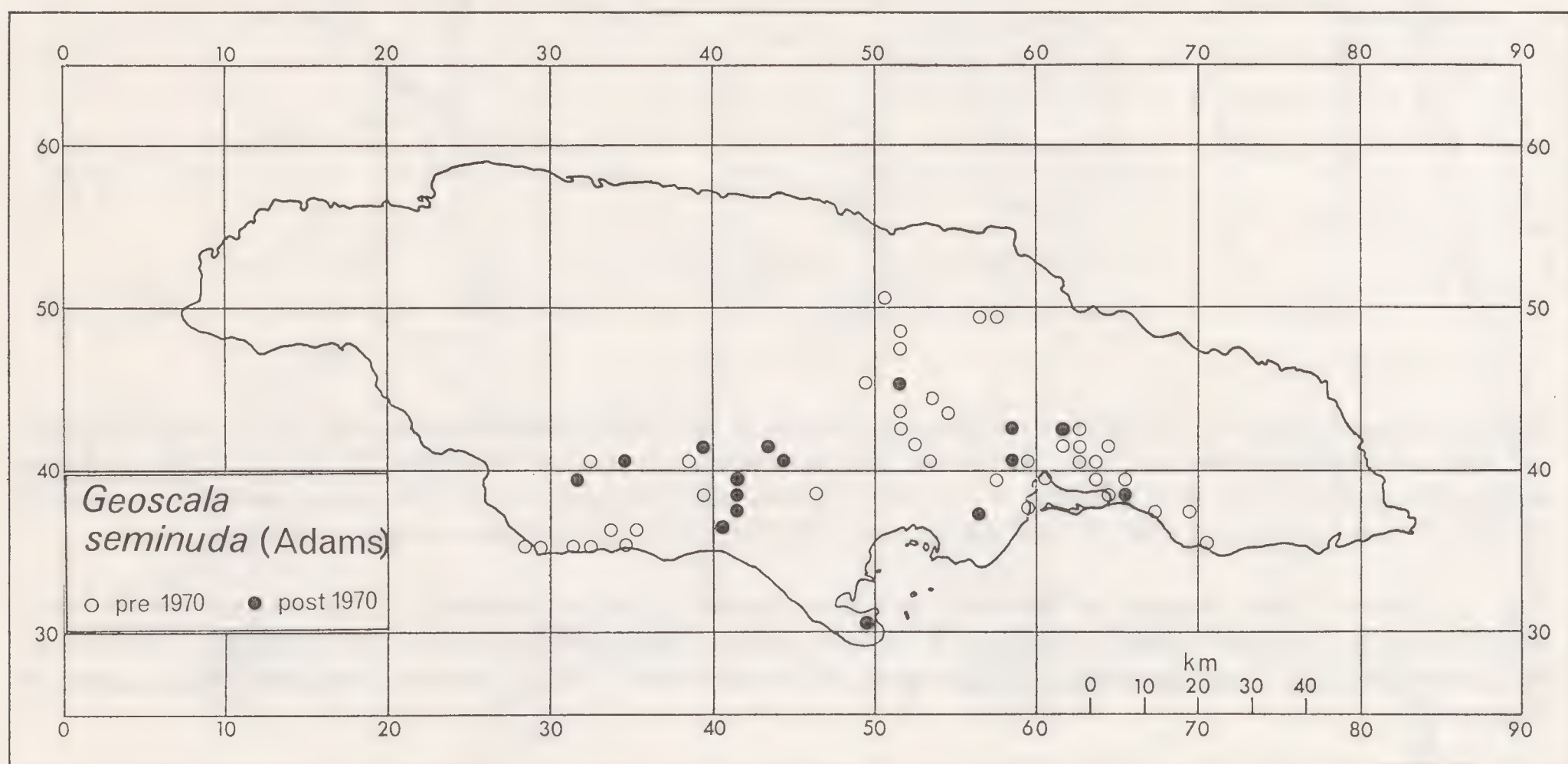


Fig. 5. Distribution map for *Geoscala seminuda* (C. B. Adams)

*Geoscala costulata* (C. B. Adams 1849) Plate 1, figs. 4–9; plate 2, figs. 5, 9, 13; plate 3, figs. 1–3; plate 4, figs. 4–5; text-figures 6–9.

*Cylindrella costulata* C. B. Adams 1849: 20. Pfeiffer 1853: 574. Bland 1861: 356. Gloyne 1872: 35. Sowerby 1875: pl. 12, fig. 104. Jacobson & Boss 1973: 340, pl. 82, figs. 13.

*Urocoptis (Brachypodella) costulata* (C. B. Adams)—H. & A. Adams 1855: 176.

*Brachypodella (Geoscala) costulata* (C. B. Adams)—Pilsbry & Vanatta 1898: 279. Pilsbry 1903b: 90, pl. 5, fig. 43. Baker 1935d: 58.

*Trachelia costulata* (C. B. Adams)—Vendryes 1899: 599.

*Brachypodella (Geoscala) costulata savlamari* Baker 1935b: 139, pl. 8, fig. 3.

*Types:* *G. costulata* (C. B. Adams). lectotype MCZ 260838 (plate 1, figs. 4–6), by designation of Jacobson & Boss 1973, pl. 82, fig. 13. Paralectotypes MCZ 260839 (17 examples), MCZ 146554 (6 examples), MCZ 151784 (2 examples) and MCZ 26937 (3 examples). *G. costulata savlamari* Baker, lectotype ANSP 163928a (plate 1, figs. 7–9), herein designated. Paralectotypes ANSP 163928 (4 examples), ANSP 168226 (2 examples).

*Type localities:* Whitney Turn, Clarendon, (Jamaican co-ordinates 4141) is selected here on the grounds that Pilsbry (1903b, pl. 5, fig. 43) has figured a specimen like the lectotype from this locality, which also lies near the centre of distribution for the species. The form *savlamari* Baker has as its type locality 'Headwaters of the Sweetwater R. and surrounding hills. Westmoreland' (Jamaican co-ordinates 1648).



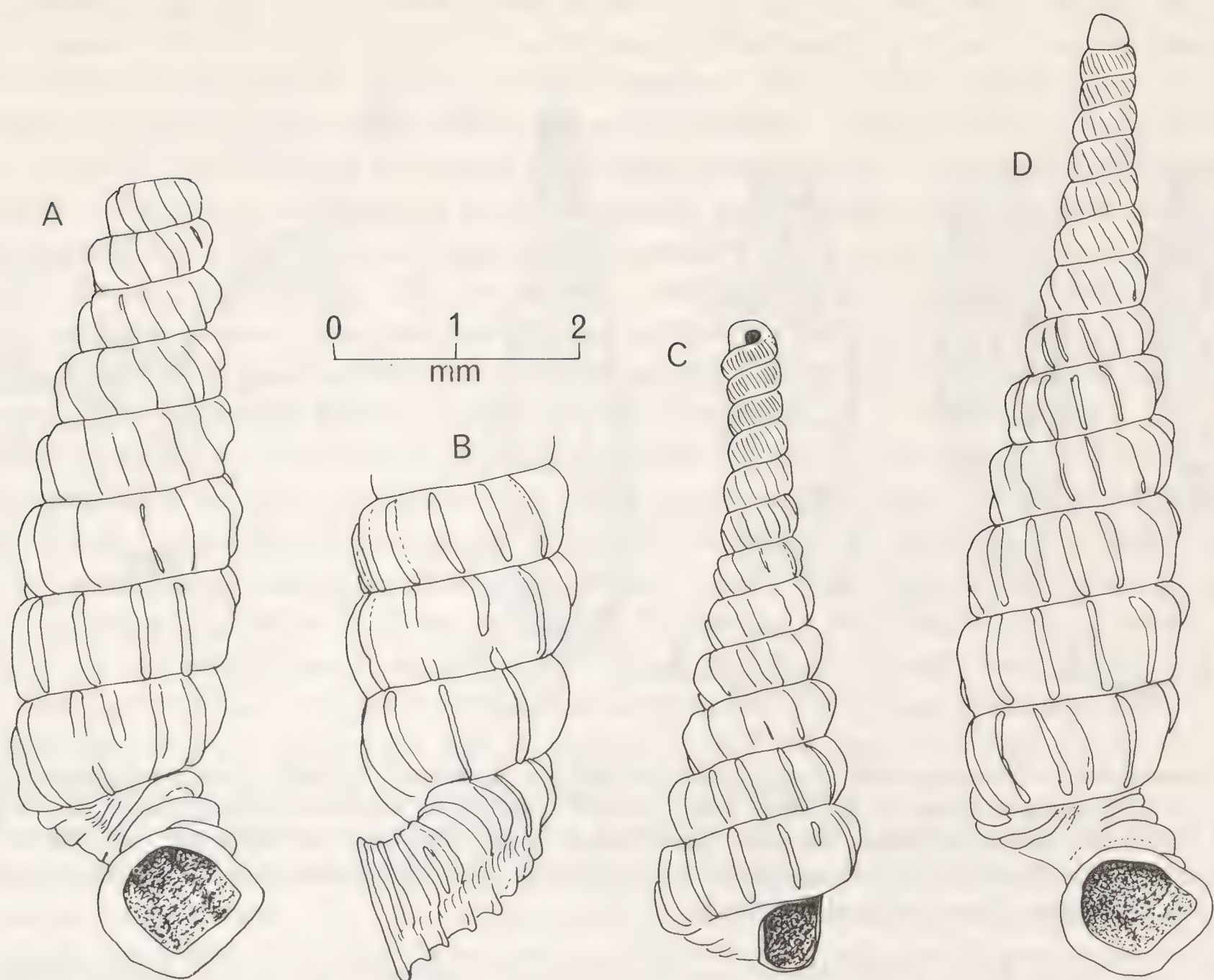


Fig. 6. Camera lucida drawings of shells of *Geoscala costulata* (C. B. Adams). A-B, lectotype MCZ 260838, apertural and lateral views,  $\alpha=19^\circ$ . C, paralectotype MCZ 146554a, a juvenile shell, D, MCZ 100890 Somerset, Manchester (H. B. Baker coll.), a complete shell.

### Description.

a. Shell: fusiform, small ( $5\frac{1}{2}$ – $6\frac{1}{2}$  mm decollate, 9 mm complete), moderately elongate (height/diameter about 2.5 in adults), normally decollate with the last quarter whorl free. Surface of mature shell ornamented with widely spaced continuous white ribs (plate 2, fig. 13) which vary from nine to twenty on the penultimate whorl. Shells are transparent white when fresh, becoming opaque with age (cf Plate 1, figs. 4–6, with 7–9).

Adults retain 7–9 whorls, complete shells have 14–15 (MCZ 100890, BMNH 54.4.19.346, figs. 6d and 7d respectively). As many as 10 juvenile whorls may be lost. The whorl outline remains convex throughout, later whorls do not become square as in the other two species. The suture is moderate and the whorls never become deeply undercut as in *G. seminuda* (figs. 6–7). The uncoiled portion of the shell has two keels and a moderately deep sulcus between them (figs. 6b, 7b–c).

The protoconch is small, high-sided initially, perforate and it bears very definite fine ridges (plate 2, figs. 5, 9). The nepionic shell consists of three whorls which are followed by 5–7 progressively more strongly striate juvenile whorls. The typical adult ribbing may start after only 3–4 juvenile whorls.

The aperture is entire (plate 3, fig. 2), free in mature adults and diamond-shaped in outline. The two keels produce the angles. The lip is reflected all round, but a little more so below (i.e. anteriorly). The body whorl does not expand significantly and the lip is scarcely thickened. The plane of the aperture lies at an angle of  $15$ – $20^\circ$  to the axis.

The periostracum is pitted, but more irregularly than in the other two species (cf. plate 3, fig. 3 with figs. 4 and 8). Internally the columella is simple and not thickened



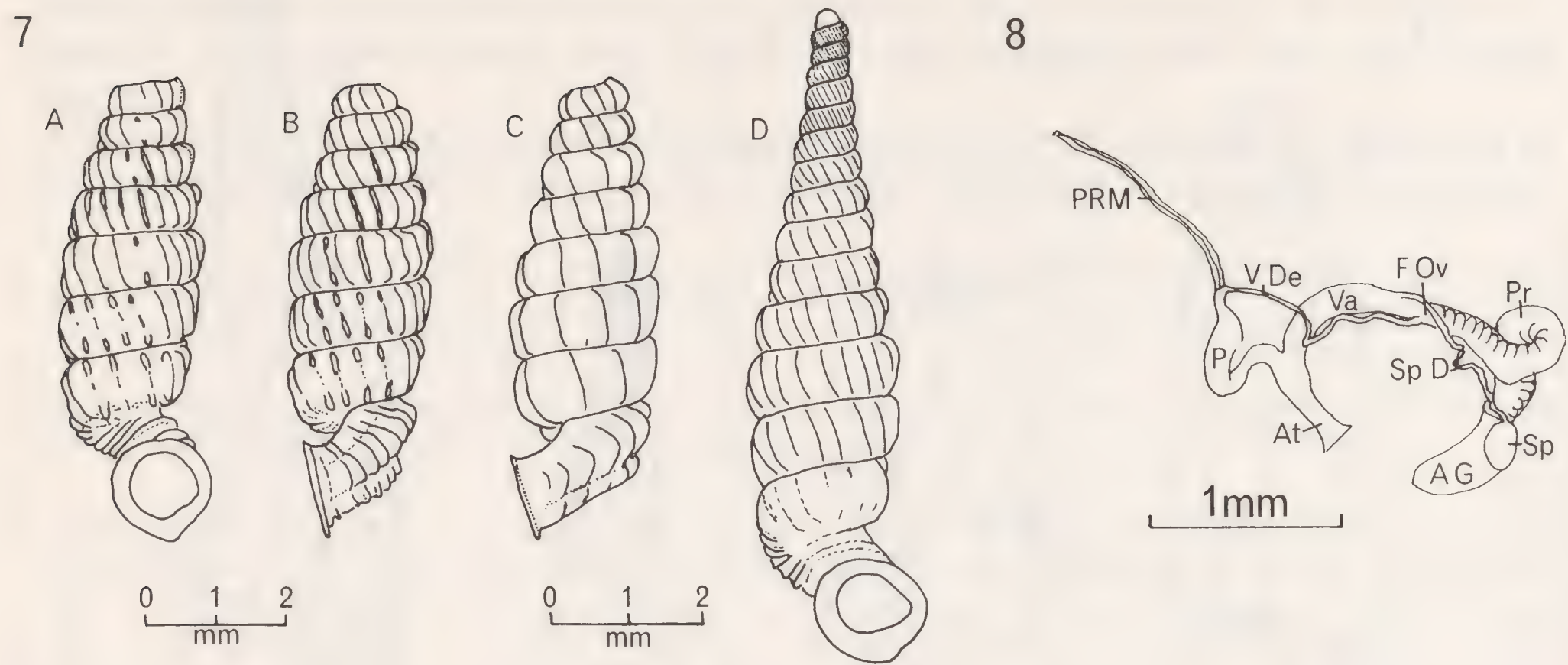


Fig. 7. Camera lucida drawings of shells of *Geoscala costulata* (C. B. Adams) to show variation in ribbing and  $\alpha$ . A-B, lectotype of *G. costulata savlamari* H. B. Baker ANSP 163928a, apertural and lateral views,  $\alpha=16^\circ$ . C, 1st Chitty coll. BMNH 54.419.346 with nine ribs on the penultimate whorl and  $\alpha=20\frac{1}{2}^\circ$ . D, 1st Chitty coll. BMNH 54.4.19.347, a complete shell with 20 ribs on the penultimate whorl. (C and D come from the same lot in the Chitty collection and presumably, therefore, from the same locality.)

Fig. 8. Camera lucida drawing of the distal genitalia of *Geoscala costulata* (C. B. Adams), Mount Diablo, St. Ann. Symbols as in fig. 4. Penial retractor separated from prostate for clarity.

TABLE 2

Measurements in *Geoscala costulata* (C. B. Adams)

Specimen	Height (mm)	Diameter (mm)	Whorls	Ribs	$\alpha$
Lectotype MCZ 260838	6.6	1.9	$8\frac{1}{4}$	10	$20^\circ$
Lectotype, <i>savlamari</i> ANSP 163928a	6.7	2.0	$7\frac{1}{4}$	16	$18^\circ$
1st Chitty coll. BMNH 54.4.19.346	8.5*	2.0	15*	20	$20^\circ$
1st Chitty coll. BMNH 54.4.19.347	7.0	—	$8\frac{1}{2}$	16	—
1st Chitty coll. BMNH 54.4.19.348	6.5	—	8	15	—
1st Chitty coll. BMNH 54.4.19.349	6.5	—	$7\frac{3}{4}$	9	—
C. Paul coll. Boston Bay, Portland	6.2	1.9	$7\frac{3}{4}$	12	$17^\circ$
C. Paul coll. Phoenix Park House, St. Ann	6.1	2.0	$8\frac{1}{4}$	15	$23^\circ$
C. Paul coll. Phoenix Park House, St. Ann	6.9	2.1	8	11	$20^\circ$
C. Paul coll. Phoenix Park House, St. Ann	6.2	2.2	$8\frac{1}{4}$	11	$30^\circ$
C. Paul coll. Cave River, Clarendon	7.3	2.3	$8\frac{1}{4}$	15	$17\frac{1}{2}^\circ$
C. Paul coll. Cave River Clarendon	7.1	2.2	8	15	—

\*This shell complete.



b. Anatomy (fig. 8): apart from being smaller, the genital anatomy seems to be very similar to that of the other two species. If anything, the atrium is proportionately longer and the free oviduct even shorter than in either congener, but too few dissections have been performed to be certain these slight differences are constant. The radula is about 3.5 by 0.12 mm, has about 70 rows of teeth arranged in the same formula as *G. seminuda* and is generally very similar. The centrals, laterals and marginals are virtually identical to those of *G. seminuda* (plate 4, figs. 4–5), but are consistently smaller; the central being about 8  $\mu\text{m}$  wide, the laterals about 25  $\mu\text{m}$  wide. The jaw is also much the same as in *G. seminuda*.

*Ecology*: *G. costulata* is more typical of wet limestone forest, but its range overlaps with that of *G. seminuda*. It is also typical of limestone outcrops and I always found it on rock surfaces and solution hollows, although Baker (1935d, p. 58) records it as a weak climber.

*Distribution*: *G. costulata* occurs throughout the central region of Jamaica from Westmoreland to St. Thomas and Portland parishes, but only rarely occurs near the coast (fig. 9).

*Variation*: Adult, decollate shells range from 6.2–7.0 mm high and 1.9–2.0 mm diameter (Table 2). Occasional complete examples reach 7.9–8.5 mm high with 14 or 15 whorls. Ribbing is more variable in its density than in *G. seminuda* and there may be from nine to twenty ribs on the penultimate whorl. The ribs occasionally divide into upper and lower portions, but most remain complete even on lower whorls. The plane of the aperture seems to vary in orientation very little and lies at about 17–20° to the axis. The suture is always moderately deep and does not vary like that of *G. seminuda*.

*Remarks*: As with *G. seminuda*, towards the western end of its range, *G. costulata* differs somewhat from the main population. H. B. Baker (1935b, p. 139) distinguished these shells as the subspecies *savlamari*. They are supposedly typified by shallower sutures, more ribs (18 on the penultimate whorl) and the ribs tend to divide into upper and lower series. While all these details are true for at least some of the shells from Westmoreland, the lectotype of *G. costulata* has some ribs which are divided into upper and lower portions (Plate 1, fig. 4) and other lots show that the number of ribs on the penultimate whorl may vary from 9–16 in any one locality and occasionally reaches 20. There does not seem to be sufficient difference in morphology to separate these western shells as a subspecies.

*G. costulata* is not easy to confuse with the other species, although I have seen one misidentified lot from Moneague, St. Ann. Its small size and continuous ribs are usually adequate to recognize it.

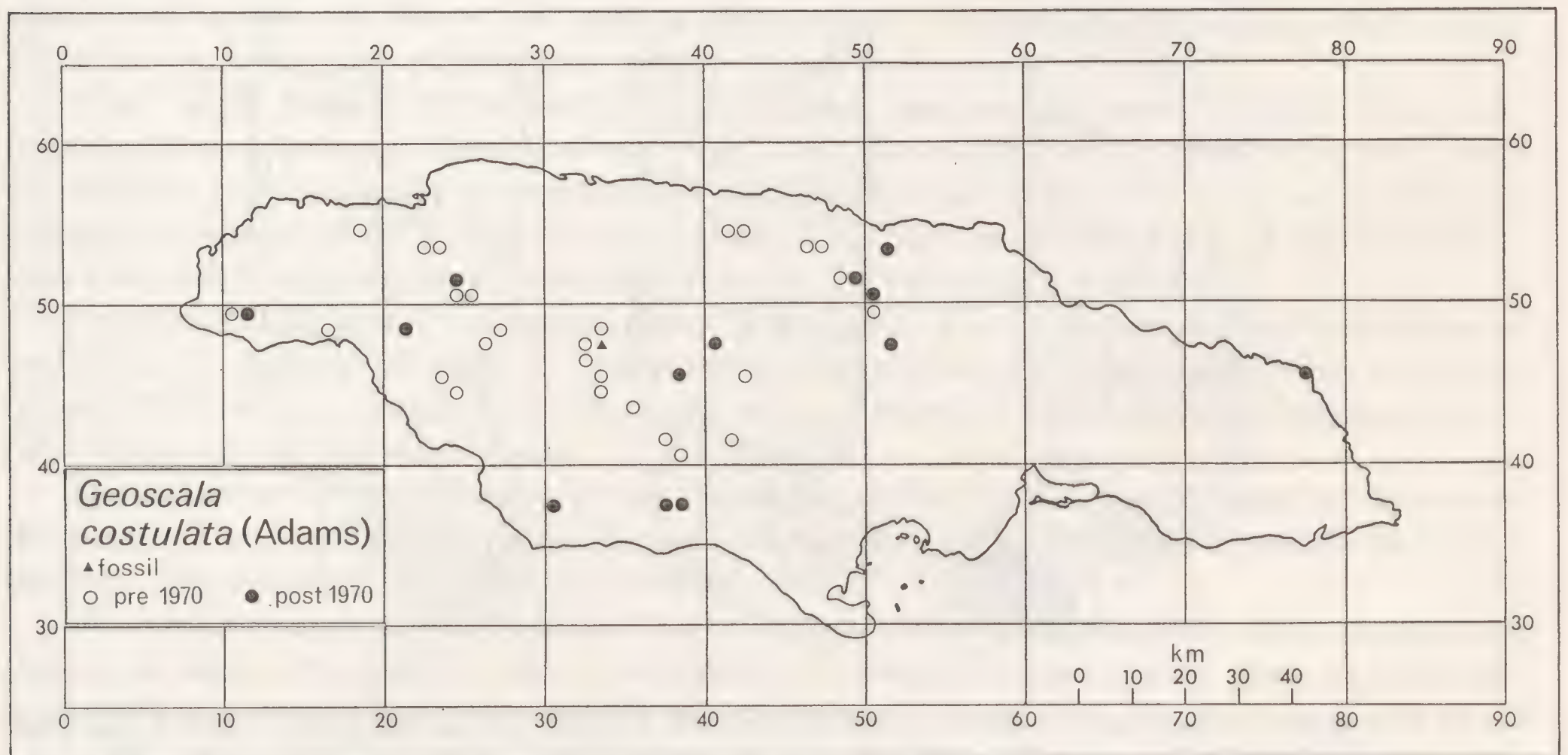


Fig. 9. Distribution map for *Geoscala costulata* (C. B. Adams).



*Geoscala robertsi* (C. B. Adams 1851) Plate 1, figs. 10–12; plate 2, figs. 6, 10, 14; plate 3, figs. 7–9; plate 4, figs. 6–9; text-figs. 10–13.

*Cylindrella robertsi* C. B. Adams 1851a (April): 160. Adams 1851b (May): 84. Pfeiffer 1853: 575. Bland 1861: 356. Gloyne 1875: 122. Sowerby 1875: pl. 12, fig. 111. Henderson 1894b: 20. Jacobson & Boss 1973: 415, pl. 61, fig. 16.

*Urocoptis* (*Brachypodella*) *robertsi* (C. B. Adams)—H. & A. Adams 1855: 177.

*Brachypodella* (*Geoscala*) *robertsi* (C. B. Adams)—Pilsbry & Vanatta 1898: 279. Pilsbry 1903b: 91, pl. 5, figs. 45–46. Baker 1935d: 58.

*Mychostoma robertsi* (C. B. Adams)—Vendryes 1899: 599.

*Brachypodella robertsi* (C. B. Adams)—Pilsbry & Brown 1911: 574.

*Types*: Lectotype MCZ 146552, (plate 1, figs. 10–12), by designation of Jacobson & Boss (1973, pl. 61, fig. 16). Paralectotypes MCZ 275733 (3 examples). The specimen selected as lectotype does not agree well with the original description in that the ribs are largely continuous across the whorls, however the paralectotypes do fit this description.

*Type locality*: near Rio Bueno, Trelawny (Jamaican co-ordinates 3956) is here selected on the grounds that it is known that Adams visited the area (Jacobson & Boss, map 1, p. 309) and that it is the first locality to be reported in the literature (Gloyne 1875, p. 122). It is also well within the known limits of distribution of *G. robertsi*.

### Description.

a. Shell: fusiform, small (8–10 mm decollate, 11–12 mm complete), moderately elongate (height/diameter about 3.5), decollate and with the last quarter whorl free. Surface of adult

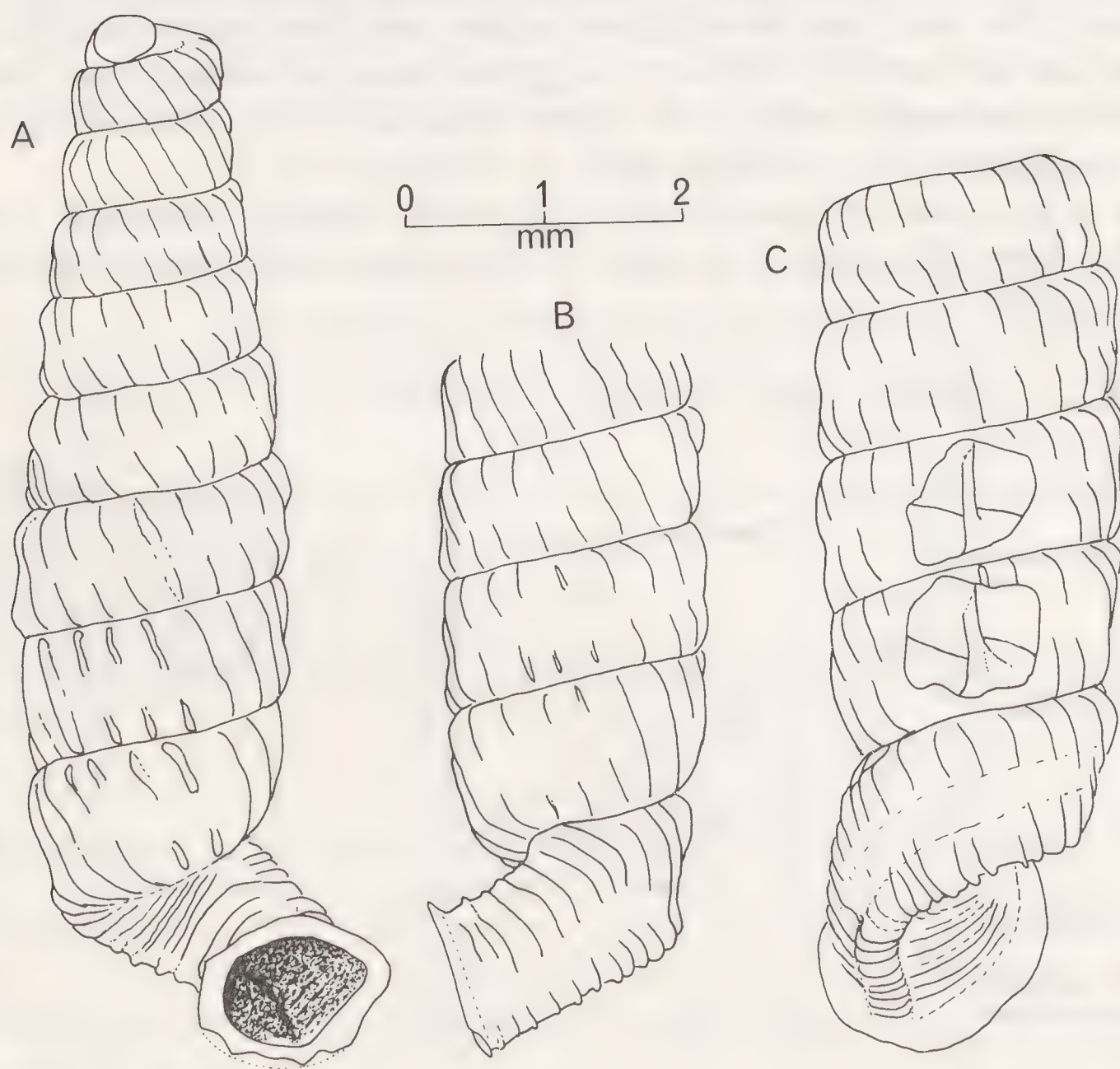


Fig. 10. Camera lucida drawings of shells of *Geoscala robertsi* (C. B. Adams). A-B, lectotype MCZ 146552, apertural and lateral views,  $\alpha=17^\circ$ . C, paralectotype MCZ 275733, a damaged shell showing the simple columella and the pair of keels on the neck of the shell.



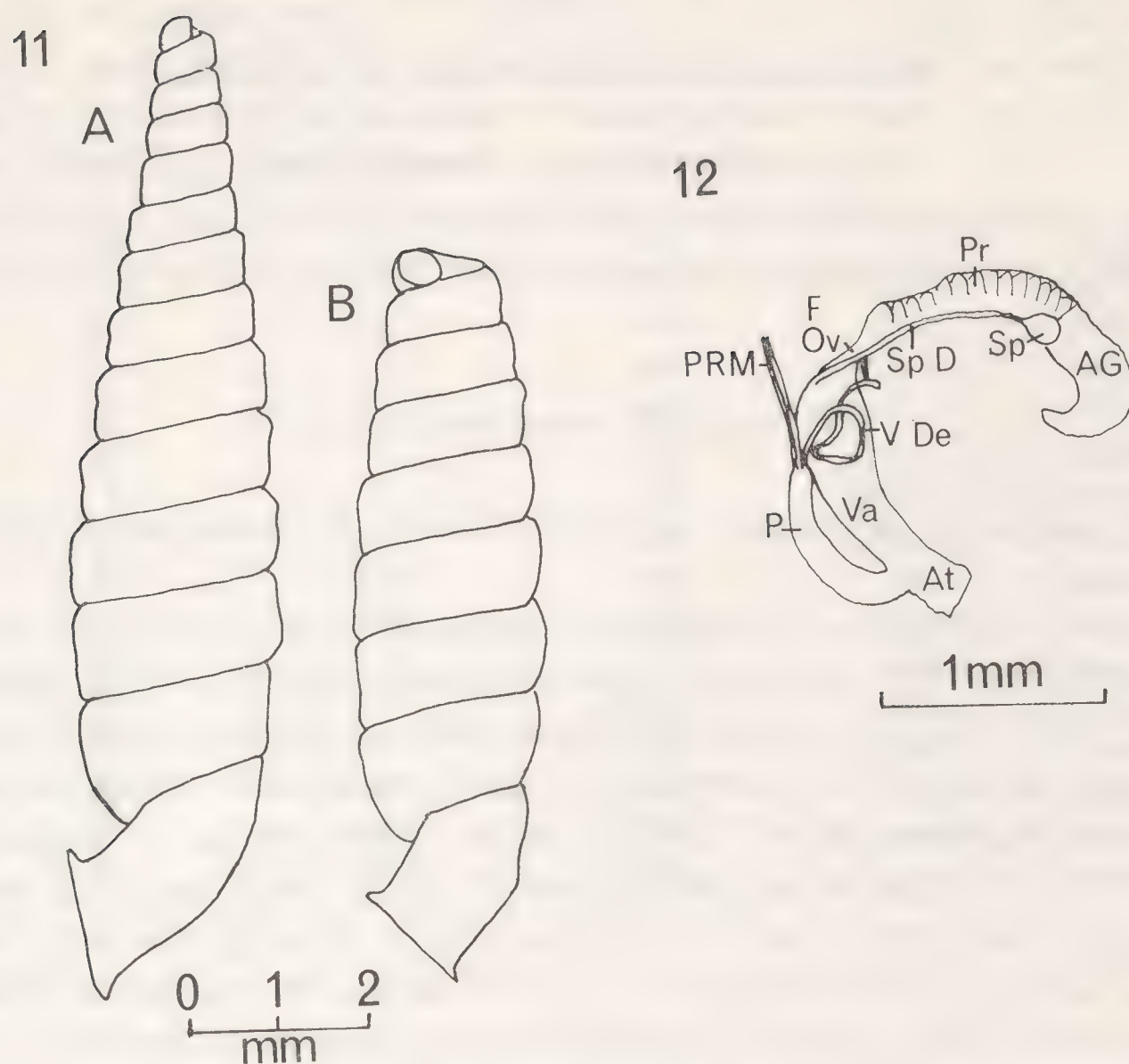


Fig. 11. Camera lucida drawings of shells of *Geoscala robertsi* (C. B. Adams) to show variation in  $\alpha$ . A, 1st Chitty coll. BMNH 54.4.19.352, a complete shell,  $\alpha=13^\circ$ . B, 2nd Chitty coll. BMNH 57.12.1.524a,  $\alpha=48^\circ$ , an exceptionally high value.

Fig. 12. Camera lucida drawing of the distal genital anatomy of *Geoscala robertsi* (C. B. Adams), Runaway Grotto, St. Ann. Symbols as in fig. 4. Penial retractor separated from prostate for clarity.

shell ornamented with prominent opaque ribs above and below the periphery as in *G. seminuda*, although in some individuals, including the lectotype, the ribs remain united. In all shells both upper and lower ribs tend to unite on the free portion of the last whorl. Shell translucent white when fresh, but opaque in old and dead specimens.

Adult shell retains 8–9 whorls, while 7–8 are lost in the juvenile shell. Complete individuals occur with 13–14 whorls (e.g. fig. 11a). The outline of the whorls is square, as in *G. seminuda*, but the suture is very shallow and there is no tendency for the lower whorls to become undercut (plate 1, figs. 10–12; text-fig. 10). The uncoiled portion of the last whorl bears two keels that are less prominent than in the other two species.

Protoconch is typical for *Geoscala* (plate 2, figs. 6, 10). The nepionic shell is about 3 whorls and is less strongly ridged than *G. costulata*. Whorls of the juvenile shell are rounded in outline initially, but become square with continuous ribs at about 6–7 whorls and the double series of ribs begins about one whorl later.

The aperture is free with a reflected lip all round. It is not expanded and the lip is not thickened. The outline is diamond-shaped, planar, the plane orientated at about  $14\text{--}20^\circ$  to the axis, but occasionally much higher (fig. 11b).

The periostracum is pitted (plate 3, figs. 7–9) and more evenly so than in *G. costulata*. In this as in other respects, *G. robertsi* resembles *G. seminuda* more closely than *G. costulata*. Internally the columella is simple and not thickened.

b. Anatomy: poorly known, but in general similar to the other two species. My specimens preserved insufficient detail for accurate comparisons. The radula reaches 5.0 by 0.15 mm

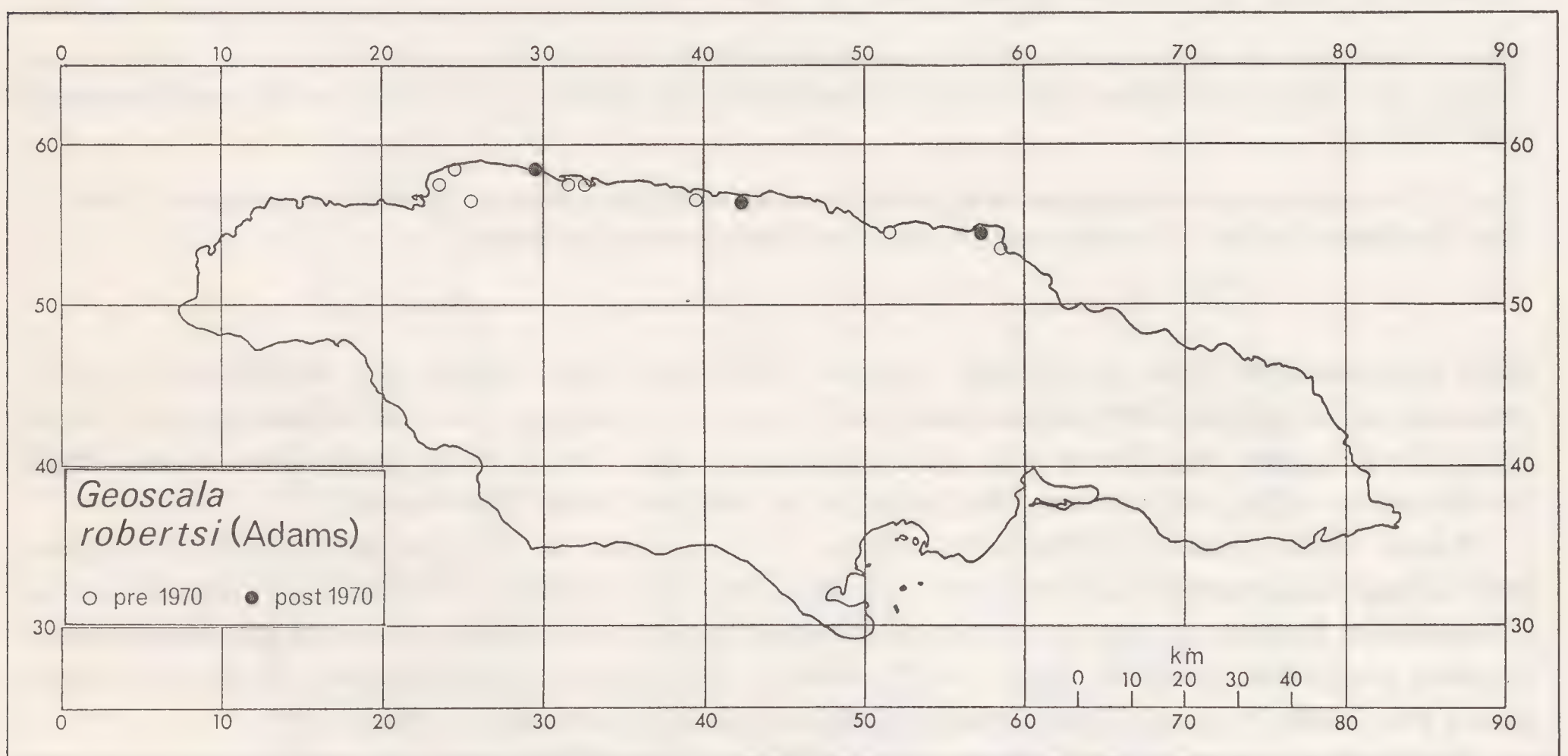


TABLE 3

Measurements in *Geoscala robertsi* (C. B. Adams)

Specimen	Height (mm)	Diameter (mm)	Whorls	Ribs	$\alpha$
Lectotype MCZ 146552	7.6	2.0	8½	20	17°
1st Chitty coll. BMNH 54.4.19.352	11.0*	2.25	13½*	19	14°
1st Chitty coll. BMNH 54.4.19.353	9.8	2.3	9¼	18	—
2nd Chitty coll. BMNH 57.12.1.524a	8.0	—	8¼	22	—
2nd Chitty coll. BMNH 57.12.1.524b	7.5	—	8¼	14	—
2nd Chitty coll. BMNH 57.12.1.524c	8.0	—	8¼	16	—
2nd Chitty coll. BMNH 57.12.1.524d	8.0	—	8	21	38°
2nd Chitty coll. BMNH 57.12.1.524e	8.75	—	7¾	22	—
C Paul coll. Greenwood, St. James	9.9	2.5	8¾	22	24°
C Paul coll. Greenwood, St. James	10.0	2.4	9	21	16°
C Paul coll. Greenwood, St. James	9.0	2.7	8½	18	10½°
C Paul coll. Greenwood, St. James	13.0*	2.4	17½*	23	8½°
C. Paul coll. Greenwood, St. James	8.8	2.7	8½	17	20½°
C. Paul coll. Rockmore, St. Mary	8.0	2.25	8½	20	20½°
C. Paul coll. Rockmore, St. Mary	8.5	2.3	8¾	15	23°
C. Paul coll. Rockmore, St. Mary	8.8	2.2	8½	22	22½°

\*These shells complete.

Fig. 13. Distribution map for *Geoscala robertsi* (C. B. Adams).

and has 80+ rows of teeth in the usual formula. The central is weakly bilobed and appears folded in on itself, the laterals are much the same as in the other two species, as are the marginals. The central is 10  $\mu\text{m}$  wide and the laterals 25  $\mu\text{m}$ . The jaw is indistinguishable from those of *G. seminuda* and *G. costulata*.

*Ecology:* *G. robertsi* is confined to limestone outcrops in dry limestone forest along a narrow northern coastal strip from Montego Bay, St. James in the west to Port Maria, St. Mary in the east (fig. 13). It occurs typically in solution hollows in rock outcrops below or along the first inland cliff line.



*Variation:* Adult, decollate shells range from 7.6–9.8 mm in height and 2.0–2.3 mm in diameter (Table 3). Complete examples reach 12.2 mm with 17 or more whorls. Ribbing is moderately variable and ranges from 14–22 ribs on the penultimate whorl. The angle of the aperture plane varies little except for odd individuals in which it may reach very high angles, 47° being the highest recorded so far. The suture is consistently shallow.

*Remarks:* The relatively large size (for *Geoscala*) shallow suture and double series of ribs serve to identify *G. robertsi*. It is the least variable and most geographically confined of the three species.

### Genus *Simplicervix* Pilsbry 1903

*Type species:* *Cylindrella inornata* C. B. Adams 1849, by original designation (Pilsbry 1903b, p. 94).

*Definition:* A genus of Apominae with small, decollate dextral shell. 7–10 rounded whorls remain in the adult shell which ranges from 5–11 mm high. The last whorl is only slightly uncoiled and may or may not bear a weak basal keel which scarcely affects the outline of the aperture. All post-nepionic whorls are densely and evenly striate, with sharp-crested ridges separated by troughs 3–5 times as wide as the ridges. The suture is moderately deep and all whorls are convex. The aperture is free, although only just in some examples, rounded, very slightly expanded and the lip only weakly reflected. The orientation of the aperture plane varies from parallel to the axis to about 45° to it. Internally the columella is simple, slightly sinuous, but not thickened. The apex is keeled above initially, perforate and the first  $\frac{1}{2}$  whorl is smooth. Thereafter fine, regular, closely spaced ribs commence. The nepionic shell is just over three whorls and is almost cylindrical in profile. Juvenile whorls expand slowly and regularly, gradually increasing in the coarseness of their striation and there are 7–8 of them.

The body of *Simplicervix* is very similar to that of *Geoscala*, even down to the unusual dark streaks on the mantle within the shell whose positions resemble those of the two series of ribs that characterize the shell of *Geoscala*. Internally, *Simplicervix* is characterized by distal genitalia that are proportionately shorter and fatter than those of *Geoscala*. The right ocular retractor is attached to the tip of the *vagina* and the free oviduct is proportionately longer. The radula is also very long and thin (6.3 × 0.22 mm) and has 80+ rows of teeth with a formula 5:2:1:2:5. The individual teeth differ in shape and proportion so that a *Geoscala* radula is immediately distinguishable from one of *Simplicervix*. The central is very weakly trilobed, not bilobed, and about 12 µm wide. The laterals are rounded, but shorter and more asymmetrical than those of *Geoscala*. The inner edge is concave and the outer more obviously convex so that the inner laterals meet to form an almost continuous scraping surface (plate 4, fig. 10). Laterals are 45 µm wide and the widest part is very close to the functional edge, whereas in *Geoscala* both edges are convex and the widest part is about half way from the base plate to the scraping edge. Outer laterals have an obsolete ectocone. The marginals are similar to those of *Geoscala*, but there is one more of them. As with *Geoscala*, cusps of all teeth are smooth and gently rounded. Although both ocular retractors are associated with the pharyngeal retractor in *Geoscala* and *Simplicervix*, the details differ. In the latter genus the columellar muscle gives rise to one muscle band which immediately bifurcates. Both resulting muscle bands then bifurcate again. The outermost pair of bands form the left and right ocular retractors, while the middle pair reunite to form the pharyngeal retractor. In both genera all divisions of the free retractor muscles occur high up, in distinction to *Apoma* where the ocular retractors separate from the pharyngeal about half way between their origin and their insertion. Anteriorly both ocular retractors split into anterior, pedal and ocular branches.



*Ecology:* *Simplicervix* lives in solution hollows in limestone outcrops within wet limestone forest of the central highlands of Jamaica. It has a distribution and habitat very similar to those of *G. costulata*, with which it often occurs. [All of the above details are based on *S. inornata*. The other two species have not been rediscovered since their original description.]

#### Key to the species of *Simplicervix*

1. Shell small (5–6 mm high), aperture plane at a high angle to shell axis (30–40°) *S. humilis*
- Shell larger (8–11 mm high), aperture plane at a low angle to shell axis (0–25°) 2
2. Shell 9–11 mm high with 7–8 whorls, common *S. inornata*
- Shell 8 mm high, 10½ whorls, very rare *S. simplex*

In *Simplicervix* the most useful characters on which to identify the shells of the three species are size, whorl number and the angle of the aperture plane. *S. humilis* is very small (5–6 mm high when decollate), has 7–8 whorls and the aperture plane lies at a high angle to the axis (33–40°). *S. inornata* is almost twice the size (9–11 mm decollate), also has 7–8 whorls and the plane of the aperture lies at 10–25° to the axis. To judge from the only known specimen, *S. simplex* is intermediate in size (8 mm high), but has 10½ whorls which are correspondingly narrower than those of the other two species, and the plane of the aperture is almost exactly parallel to the shell axis.

*Simplicervix inornata* (C. B. Adams 1849) Plate 1, fig. 16; plate 2, figs. 1–3, 7, 11; plate 3, figs. 10–12; plate 4, figs. 10–12; text-figs. 14a–e, 15–16.

*Cylindrella inornata* C. B. Adams 1849: 22. Pfeiffer 1853: 575. Bland 1861: 356. Gloyne 1872: 35. \*Sowerby 1875: pl. 11, fig. 99. Henderson 1894b: 20. Jacobson & Boss 1973: 367, pl. 61, fig. 7.

*Urocoptis (Brachypodella) inornata* (C. B. Adams)—H. & A. Adams 1855: 177.

\**Cylindrella aspera* Sowerby (non C. B. Adams) 1875: pl. 11, fig. 98.

\**Cylindrella asperata* Sowerby 1875: index to *Cylindrella* [renaming of above.]

*Brachypodella (Geoscala) inornata* (C. B. Adams)—Pilsbry & Vanatta 1898: 279.

*Mychostoma inornata* (C. B. Adams)—Vendryes 1899: 599.

*Brachypodella (Simplicervix) inornata* (C. B. Adams)—Pilsbry 1903b: 94, pl. 5, figs. 40, 47–49. Thiele 1931: 675. Zilch 1960: 542, fig. 1896.

*Types:* Lectotype MCZ 155907, by designation of Jacobson and Boss 1973, pl. 61, fig. 7. Paralectotypes MCZ 275693 (2 examples, Chitty coll.), MCZ 146549 (3 examples, Bland coll.), MCZ 155908 (1 example, Adams coll.). When I examined the collections in the Museum of Comparative Zoology in August 1977, the lectotype had been damaged at some time since it was photographed by Jacobson & Boss. For this reason, one of the paralectotypes is figured here (plate 2, figs. 1–3).

*Type locality:* There is no available information as to where Chitty or Adams collected their material. Hence I am designating Mount Horeb, St James (Jamaican co-ordinates 248529), an area of limestone outcrop on the edge of some primary, uncut wet limestone forest, as type locality on the grounds that this is where the dissected specimens originated.

#### Description.

a. Shell: elongate-conical to fusiform, small (9–11 mm decollate). Shell ornamented with fine, blade-like ridges which are slightly oblique, concave towards the aperture and separated by rounded grooves which are about five times as wide as the ridges (plate 2, figs.

\*[Sowerby's figures are very poor and as far as I have been able to tell, both original shells have been lost.]



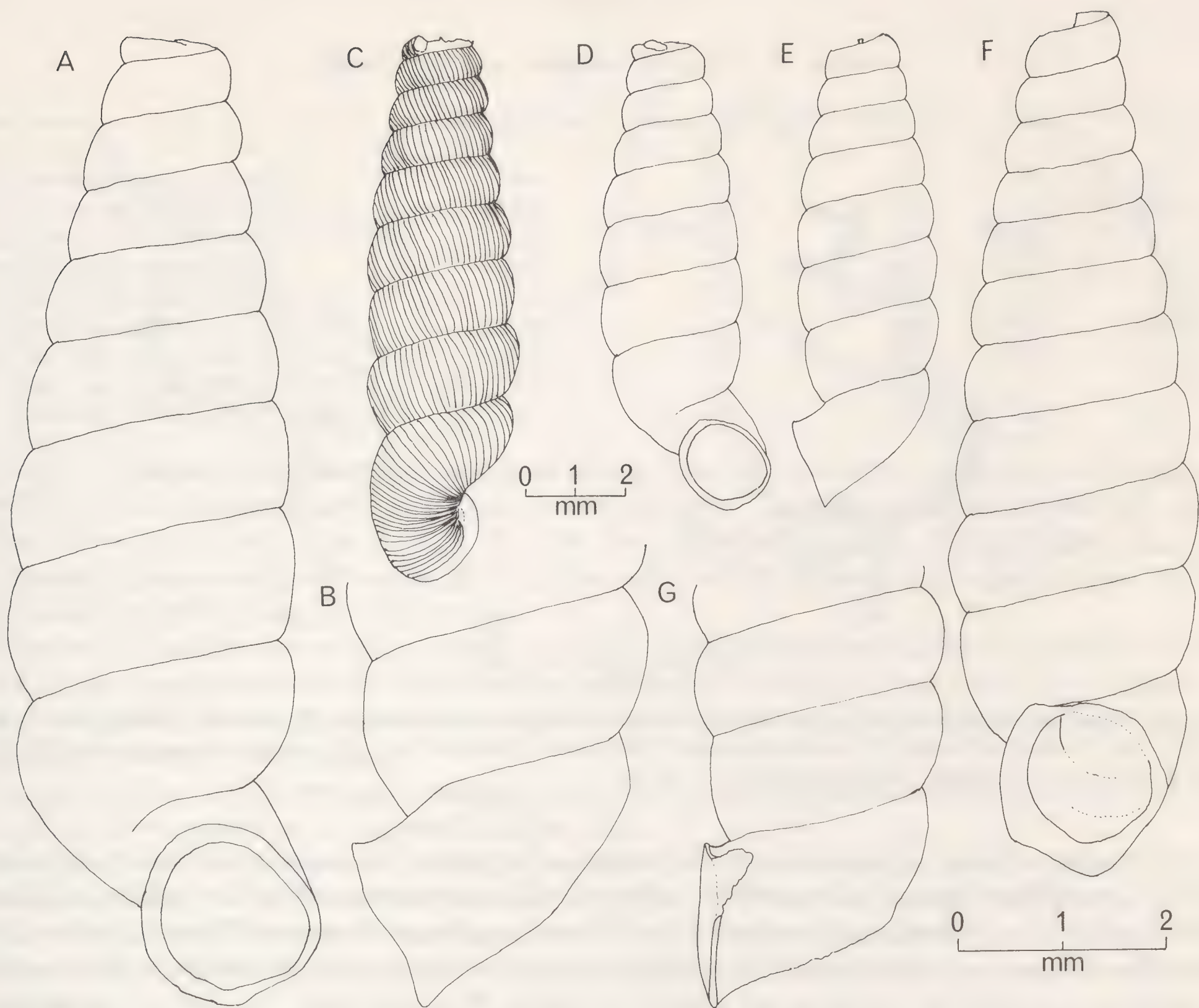


Fig. 14. Camera lucida drawings of shells of *Simplicervix* species. A-E, *Simplicervix inornata* (C. B. Adams). A-B, Paralectotype MCZ 275693a, apertural and lateral views,  $\alpha=22\frac{1}{2}^\circ$ . C, Day Kimball coll., BMNH, Hanover Parish, dorsal view to show lack of basal keel and the characteristic ribbing. D-E, 1st Chitty coll. BMNH 54.4.19.53, apertural and lateral views,  $\alpha=21^\circ$ . F-G, *Simplicervix simplex* (C. B. Adams). Lectotype MCZ 260842, apertural and lateral views.

1-3; plate 3, fig. 10). There are approximately 80 ridges on the penultimate whorl of the figured paralectotype (MCZ 275693a); 65 in BMNH 57.12.1.513a and 57 in BMNH 54.4.19.53 (text-fig. 14d-e).  $7\frac{1}{2}$ - $8\frac{3}{4}$  whorls remain in the adults and they are all regularly rounded with moderately deep sutures, the last  $\frac{1}{6}$  whorl is uncoiled and free. It retains the oblique ridges and has only the faintest trace of a basal keel. I have seen no example with an entire shell, but Pilsbry (1903b, p. 95) records one from the Clapp collection that is 12.2 mm high and has  $15\frac{1}{2}$  whorls.

The apex is much the same as those of *Geoscala* species (plate 2, figs. 7, 11), but is shorter and wider. It also has the characteristic sharp-crested ridges that typify the adult shell in *Simplicervix*.

The aperture is rounded, but with a slightly irregular outline (fig. 14a, d). The neck is scarcely expanded and the lip only slightly reflected and hardly thickened at all. The plane of the aperture lies at between  $10$  and  $25^\circ$  to the axis.

The periostracum is pitted (plate 3, fig. 12) but more finely so than in any species of *Geoscala*. It is rather irregular in development and resembles that of *G. costulata*, which lives in the same habitats as *S. inornata*, more than the pitting in the other two species of *Geoscala*. Internally the columella is simple, not thickened, but very slightly sinuous.



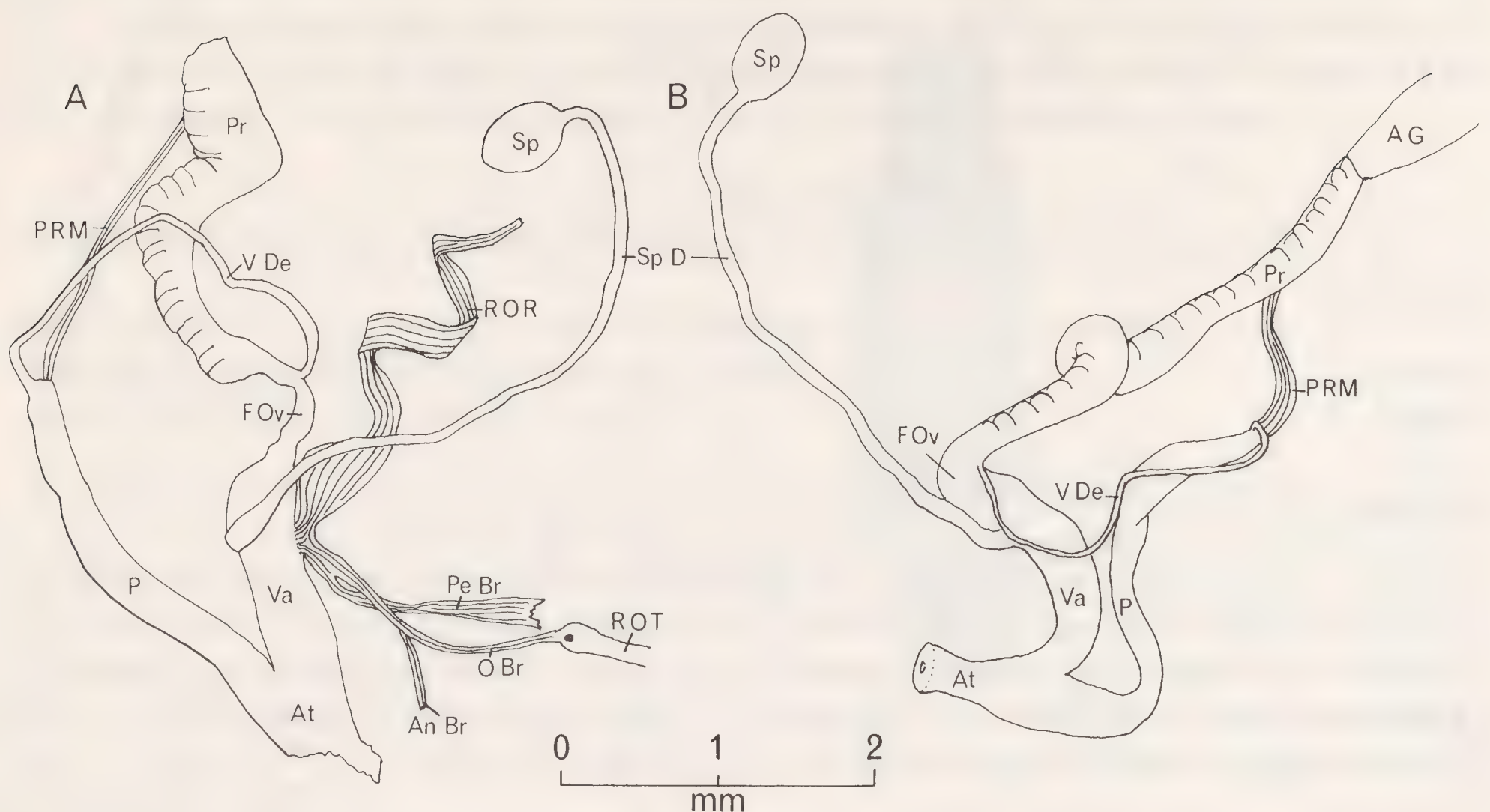


Fig. 15. Camera lucida drawings of the distal genitalia of *Simplicervix inornata* (C. B. Adams), Mount Horeb, St. James. An Br anterior branch, O Br ocular branch, Pe Br pedal branch, of the right ocular retractor muscle (ROR), ROT right ocular tentacle. Other symbols as in fig. 4.

b. *Anatomy*: Since no anatomical information whatsoever has previously been published for the genus *Simplicervix*, it is worth recording details not mentioned in the definition fairly thoroughly. The relaxed body is about 8 by 2.3 mm maximum diameter. The mantle has the irregular pigment streaks found in *Geoscala* species and there are about  $7\frac{1}{2}$  whorls. The top  $2\frac{1}{2}$  whorls are occupied by the digestive gland; the lowest  $2\frac{1}{2}$  by the lung. The foot sole is simple with transverse muscular ridges only and no foot fringe. The head has only the ocular tentacles, though sensitive spots seem to replace the lower (anterior) tentacles. The oesophagus passes through the buccal mass and nerve ring, is accompanied by two white salivary glands and ascends close to the shell axis, but outside the retractor muscles. It enters the stomach well above the apex of the lung, then there is a single short loop and the hind gut descends just below the suture. The radular sac is very prominent, passes up to and is pressed close against, the prostate.

The genitalia are as follows:— The hermaphrodite gland lies in the lower lobe of the digestive gland. The contorted hermaphrodite duct enters the prostate at the junction with the albumen gland and on the inside of the coil. The prostate is relatively large and occupies more than one whorl. Distally it gives rise to a narrow free oviduct which is proportionately longer than in *Geoscala*, but still short (0.7 mm), and a very narrow vas deferens (0.07 mm diameter). This descends, reverses its direction at a distinct angle and inserts in the tip of the penis. As with all Jamaican urocoptids, the penis lacks an epiphallus, flagellum or sheath, but in *Simplicervix* (as with other apomine genera) retains a separate penial retractor muscle that inserts on the inside of the coiled prostate. The penis is long and narrow ( $2.5 \times 0.3$  mm) and inserts into a moderate atrium ( $1.0 \times 0.3$  mm maximum diameter). The vagina is shorter and fatter than the penis ( $1.5 \times 0.5$  mm) and is bent asymmetrically by its attachment to the right ocular retractor (fig. 15a). The spermatheca duct arises from the side of the vagina, is exceedingly narrow (0.03 mm diameter), passes all the way up the prostate and ends in a small globular to oval spermatheca.

The radula and free retractor muscles are as described for the genus.



TABLE 4

Measurements in *Simplivervix inornata* (C. B. Adams)

Specimen	Height (mm)	Diameter (mm)	Whorls	Ribs	$\alpha$
Paralectotype MCZ 275693a	9.4	2.75	$8\frac{3}{4}$	80	$24^\circ$
1st Chitty coll. BMNH 54.4.19.53	9.6	2.8	$7\frac{3}{4}$	57	$21^\circ$
2nd Chitty coll. BMNH 57.12.1.513a	9.25	2.8	$7\frac{1}{2}$	65	$18^\circ$
Day Kimball coll. BMNH	10.5	3.0	$8\frac{1}{4}$	55	—
Day Kimball coll. BMNH	10.25	3.0	$8\frac{1}{4}$	—	$11^\circ$
C. Paul coll. Fern Gully, St. Ann	10.0	2.9	$7\frac{1}{4}$	71	$21\frac{1}{2}^\circ$
C. Paul coll. Fern Gully, St. Ann	10.8	3.0	$8\frac{3}{4}$	55	$19^\circ$
C. Paul coll. Fern Gully, St. Ann	10.6	—	9	—	—
C. Paul coll. Fern Gully, St. Ann	10.9	2.8	$8\frac{3}{4}$	48	$22^\circ$

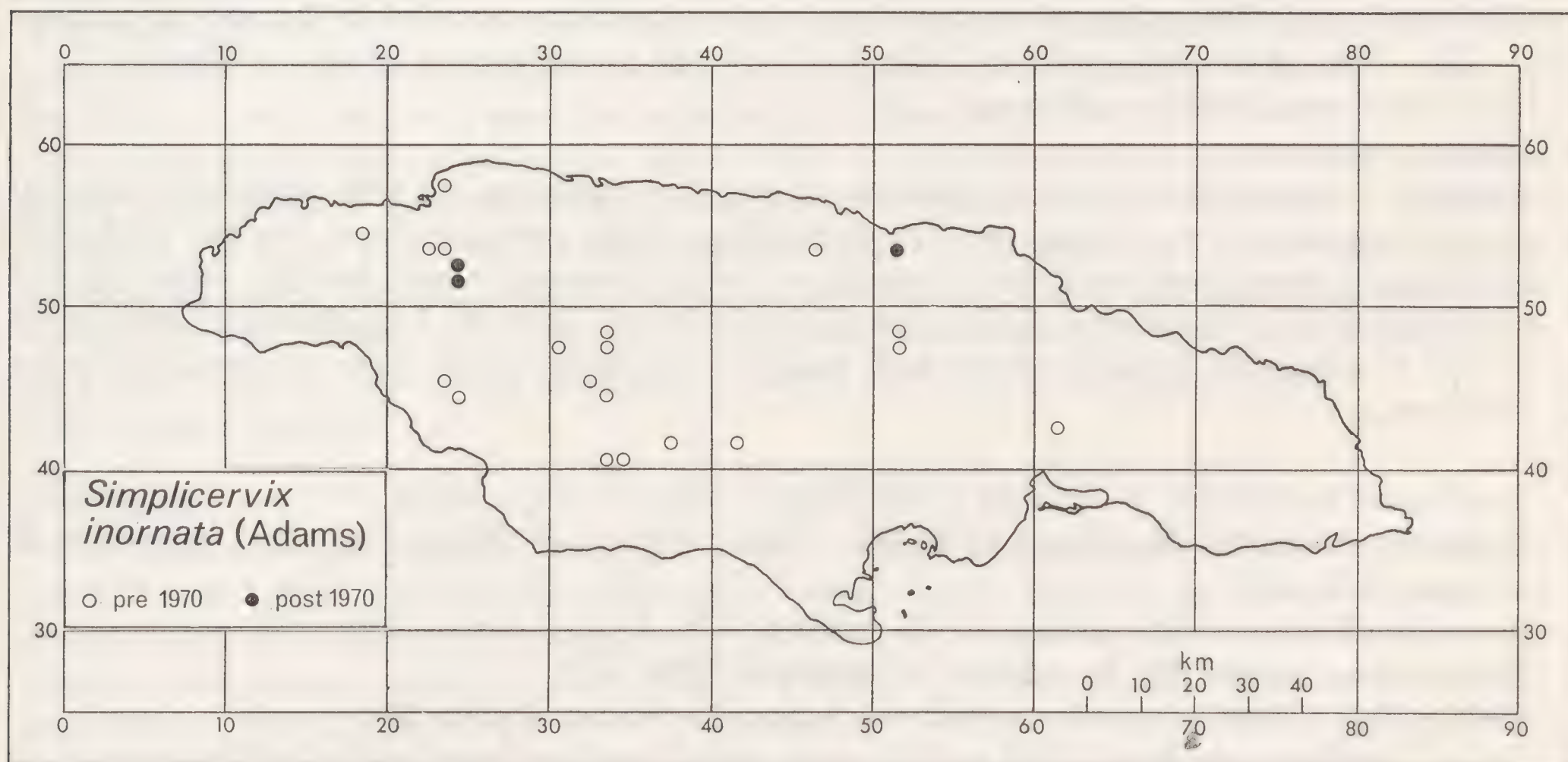
**Ecology:** *S. inornata* occurs in wet limestone forest, usually on limestone outcrops, but often under a much thicker litter cover than *Geoscala* species. This may account for the very few samples in collections that look as though they were taken alive. Great Valley Estate, Hanover (Jamaican co-ordinates 1854) is the only locality I have come across where fresh specimens seem to have been common.

**Variation:** *S. inornata* seems to be a fairly constant species. Ribbing varies from about 55–80 ribs on the penultimate whorl, shell dimensions from 9.25–10.25 mm by 2.8–3.0 mm (table 4) and the plane of the aperture from about  $10$ – $25^\circ$  to the axis, but otherwise significant variation seems to be lacking.

**Distribution** (fig. 16): *S. inornata* is widespread in the central highlands of Jamaica and, like *G. costulata*, does not seem to approach either coast.

**Remarks:** *S. inornata* is immediately distinguishable from all *Geoscala* species by its fine ribbing and lack of large white lamellae on the lower whorls. It is unlikely to be confused with its congeners, if only because no-one has found them since last century. It is very similar in proportions to *S. humilis* but about twice the size, while *S. simplex* has more and narrower whorls.

Jacobson & Boss (1973, explanation to plate 61, fig. 7) give the measurements of the now damaged lectotype as 6.4 mm high by 2.4 mm wide. Even though it is no longer possible to

Fig. 16. Distribution map for *Simplivervix inornata* (C. B. Adams).



check these measurements, they seem far too low. I have not seen an example of *S. inornata* less than about 9 mm high as an adult.

*Simplicervix simplex* (C. B. Adams 1849) Plate 1, figs. 17–19; text-figs. 14f–g.

*Cylindrella simplex* C. B. Adams 1849: 22. Pfeiffer 1853: 573. Bland 1861: 361. Jacobson & Boss 1973: 421, pl. 61, fig. 3.

*Urocoptis (Brachypodella) simplex* (C. B. Adams)—H. & A. Adams 1855: 177.

*Mychostoma simplex* (C. B. Adams)—Vendryes 1899: 599.

*Brachypodella (Simplicervix) simplex* (C. B. Adams)—Pilsbry 1903b: 95.

*Type*: Jacobson & Boss (1973, pl. 61, fig. 3) accepted the only known specimen of this species as the holotype, presumably by monotypy. However, Adams gives no indication in his original description that he had only one specimen available. The fact that *C. simplex* is listed in Adams' catalogue (Adams 1851c, p. 183, species no. 188) suggests that he may have had others for exchange or sale. I prefer to err on the side of caution and accept the specimen as the lectotype. Whatever precise status is attributed to it, currently it is the only known example of the species.

*Type locality*: Jamaica.

#### *Description.*

a. Shell: elongate-conical, small, 8.3 mm high, 2.4 mm maximum diameter and with  $10\frac{1}{2}$  whorls remaining. Ornamented with fine, closely spaced ribs, which are not as sharp-crested as those of *S. inornata* and are separated by slightly narrower and shallower grooves. The ratio of ridge width to groove width is 1:3–4. There are some 57 ridges on the penultimate whorl and their spacing is somewhat more variable than in *S. inornata*. The  $10\frac{1}{2}$  whorls which remain in the adult are proportionately narrower than those of *S. inornata*, so that they appear to be more tumid and to have slightly deeper sutures. The last  $\frac{1}{8}$  whorl is free, expands slightly towards the aperture which has a much more widely reflected lip than *S. inornata* and the last whorl bears a pronounced basal keel (plate 1, fig. 19).

The protoconch and juvenile shell are unknown.

Aperture rounded, slightly angular anteriorly due to the keel, but generally more regularly circular than in *S. inornata*. Although the lip is damaged, it is clearly more broadly reflected than in any example of *S. inornata* and, contrary to the latter species, it is not thickened at all. The plane of the aperture is almost exactly parallel to the axis of coiling.

The form of the columella and the details of the periostracum remain unknown.

b. Anatomy: totally unknown.

*Ecology*: unknown.

*Remarks*: *S. inornata* is not very variable at all and this specimen lies well outside the normal range of variation for that species. The orientation of the aperture plane, the less blade-like ribbing, the prominent basal keel, larger number of narrower whorls and the reflected, but not thickened lip, all serve to distinguish *S. simplex* from *S. inornata*. I am therefore inclined to accept *S. simplex* as a valid species and that it is either extremely rare or very local in its occurrence.

*Simplicervix humilis* (C. B. Adams 1850) Plate 1, figs. 13–15; text-fig. 17.

*Cylindrella humilis* C. B. Adams 1850: 101. Pfeiffer 1853: 573. Bland 1861: 361. Jacobson & Boss 1973: 363.

*Urocoptis (Brachypodella) humilis* (C. B. Adams)—H. & A. Adams 1855: 177.

*Gongylostoma humilis* (C. B. Adams)—Vendryes 1899: 600.

*Brachypodella (Simplicervix) humilis* (C. B. Adams)—Pilsbry 1903b: 96.

*Types*: Jacobson and Boss (1973 p. 363) were unable to trace any example of this species in Adams' collection at Harvard. The only examples that I have come across are in the second



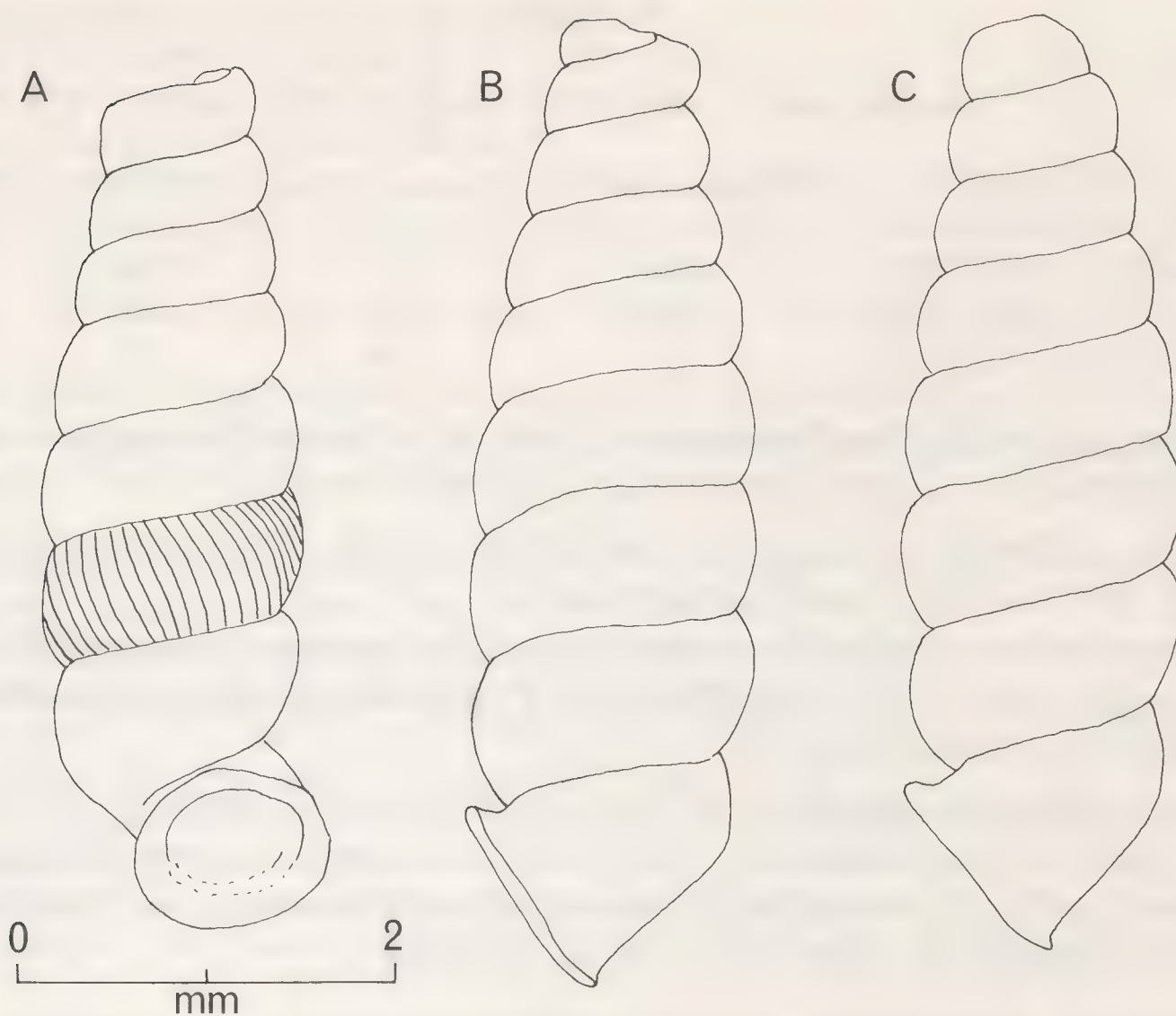


Fig. 17. Camera lucida drawings of shells of *Simplicervix humilis* (C. B. Adams), 2nd Chitty coll. BMNH 57.12.1.622a-c. A, apertural view and ribbing, B-C, lateral views to show high values of  $\alpha$ . B,  $\alpha=33^\circ$ , C,  $\alpha=39^\circ$ .

Chitty collection in the BMNH, where there are two boxes labelled ?*humilis*. One, BMNH 57.12.1.621, contains three specimens of *Spirostemma*, which I am ignoring because they do not agree with the original description at all and because Adams (1851c, p. 183, 1851d, p. 107) clearly associates *humilis* with *inornata* and *simplex* in his catalogue. The second box, BMNH 57.12.1.622, contains five miniature *Simplicervix* which are about 5 mm high. In his original description (1850, p. 101) Adams states 'Length 0.2 inch; breadth 0.05 inch'. This makes the shells about 5 mm by 1.25 mm. Pilsbry (1903b, p. 96) accepted *humilis* as a species of *Simplicervix* on the original description alone. This second box has three labels or comments. The top label states '*humilis* C B Ad Jamaica C C' and was probably added when the shells were incorporated into the main collection. The 'C C' stands for Chitty collection. The original label, now on the base of the box, states '*Cylindrella humilis*?' At some later date someone has added on the base of the box 'Sg *Simplicervix*' and 'Jamaica'. Although collected by Chitty, these specimens were not selected by Adams and so were not identified by him. They have no potential type status, but it seems to me that they are the nearest anyone is going to get towards understanding to which species the name *C. humilis* Adams should be attached. As such, I propose to base my description of *S. humilis* on them. However, the species has never been illustrated before, has never been mistakenly identified and hence there is no need to select a neotype. Finally, *Cylindrella humilis* cannot in any way be argued to be a *nomen oblitum*. The name must stand, based on Chitty's five specimens.

*Type locality*: Jamaica.

#### *Description*:

a. Shell: elongate-conical, very small (5–6 mm high in decollate adult shells), diameter 1.4–1.5 mm, with 7–8 whorls. Whorls rounded, with moderately deep sutures and ornamented with distinct fine ridges much like those of *S. inornata*, but proportionately more distinct and coarser than in the other two species. About 45–50 ridges occur on the penultimate whorl. The last  $\frac{1}{8}$  or less of the body whorl is free and the last whorl lacks a basal keel, as in *S. inornata*.

The protoconch and juvenile shell are unknown.



TABLE 5

Measurements in *Simplicervix humilis* (C. B. Adams)

Specimen	Height (mm)	Diameter (mm)	Whorls	Ribs	$\alpha$
2nd Chitty coll. BMNH 57.12.1.622a	4.7	1.4	7 $\frac{1}{4}$	—	39°
2nd Chitty coll. BMNH 57.12.1.622b	5.3	1.5	8 $\frac{1}{4}$	—	34°
2nd Chitty coll. BMNH 57.12.1.622c	4.7	1.45	7 $\frac{1}{2}$	—	36°

Aperture regularly oval, free, scarcely expanded, with the lip weakly reflected all round and forming a plane at a high angle to the axis (33–40°).

Internally the columella is scarcely thickened, simple and slightly sinuous.

b. Anatomy and ecology totally unknown.

*Variation:* as far as one can judge from five shells, this species varies as little as *S. inornata*, of which it is an almost exact miniature (Table 5). The principal difference other than size is the orientation of the aperture plane.

*Remarks:* *S. humilis* could be mistaken for a small version of *S. inornata*. If it were not that the latter species apparently varies so little, I would be inclined to accept this as a small race of *S. inornata*. However, so far I have not seen any example of *S. inornata* less than 9 mm high or with the plane of the aperture at more than 24° to the axis.

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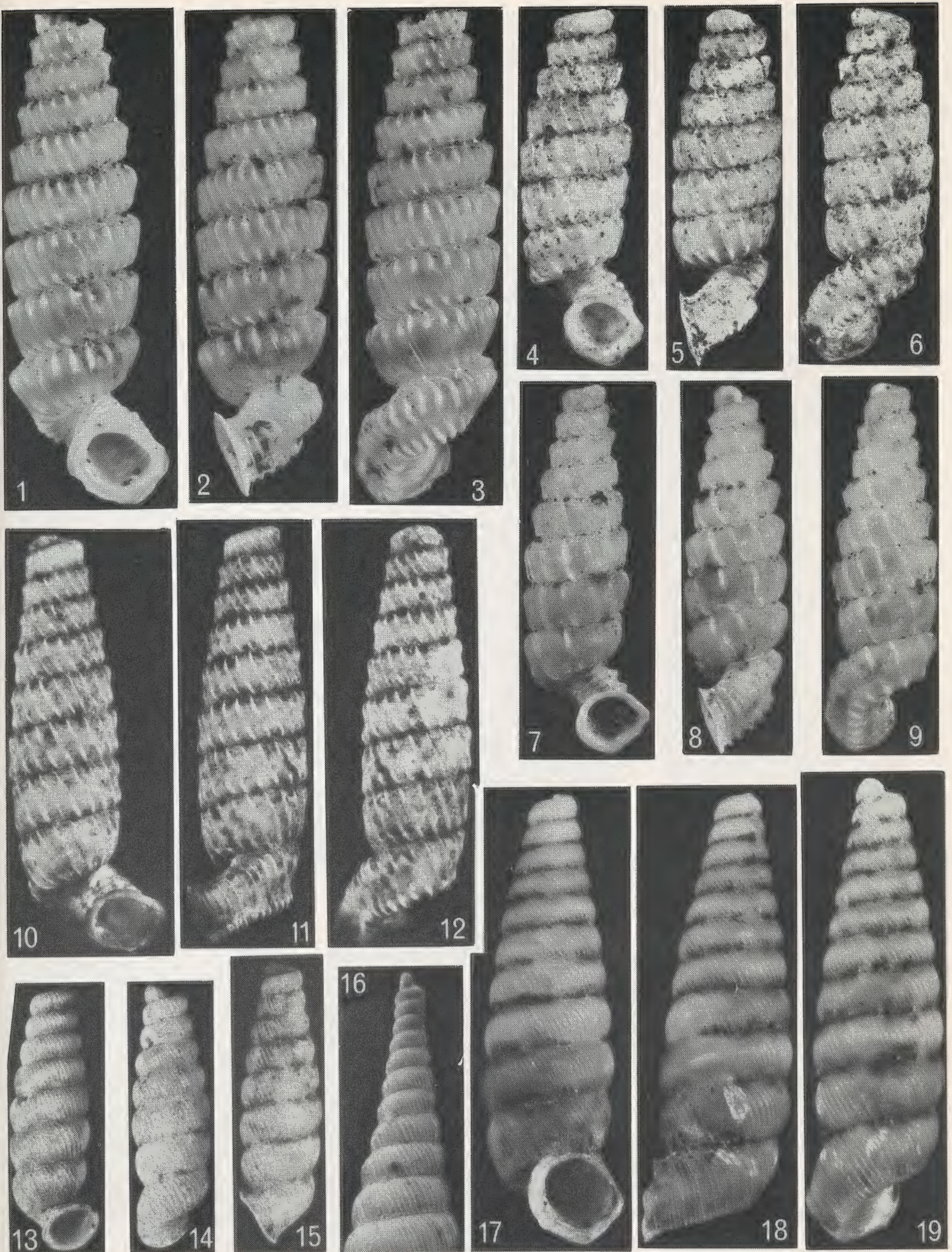
PLATE 1 TYPE SPECIMENS OF *GEOSCALA* AND *SIMPLICERVIX*

- Figs. 1–3. *Geoscala seminuda* (C. B. Adams), lectotype, MCZ 155909.  
Figs. 4–6. *Geoscala costulata* (C. B. Adams), lectotype, MCZ 260838.  
Figs. 7–9. *Geoscala costulata savlamari* H. B. Baker, lectotype. ANSP 163928.  
Figs. 10–12. *Geoscala robertsi* (C. B. Adams), lectotype, MCZ 146552.  
Figs. 13–15. *Simplicervix humilis* (C. B. Adams). BMNH 57.12.1.622 (three different shells).  
Fig. 16. *Simplicervix inornata* (C. B. Adams). Scanning electron micrograph of apical whorls and juvenile shell. Fern Gully, St. Ann.  
Figs. 17–19. *Simplicervix simplex* (C. B. Adams), lectotype, MCZ 260842.  
All figures  $\times 10$ .

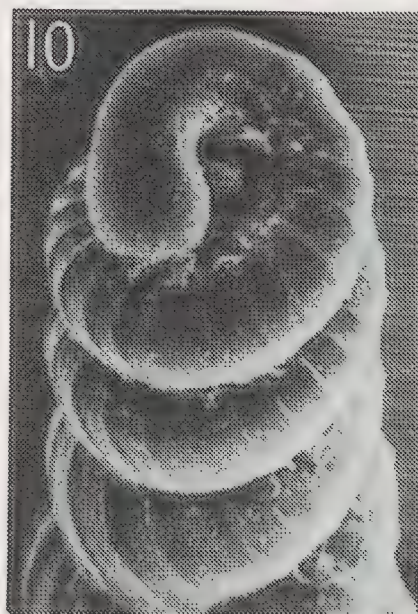
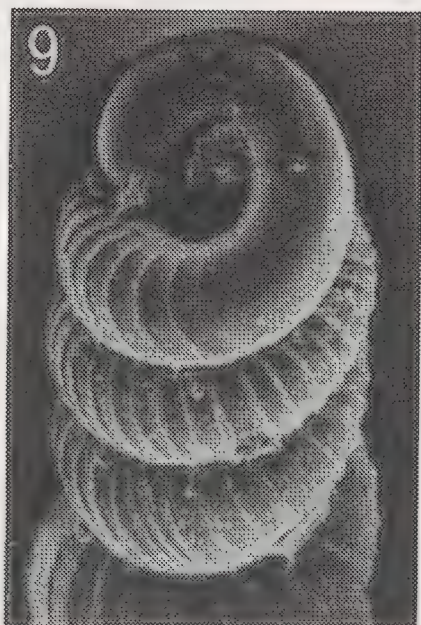
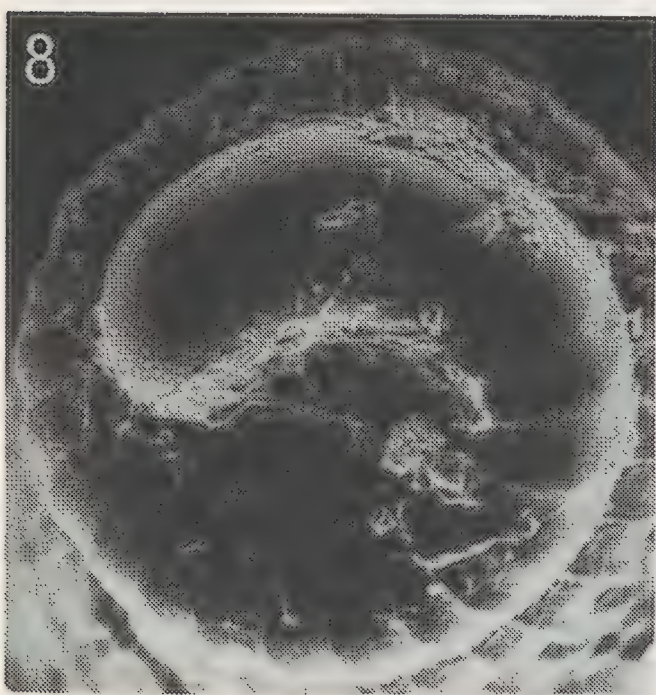
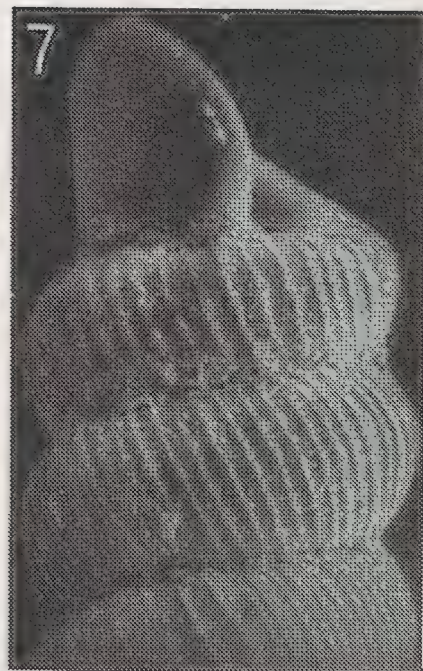
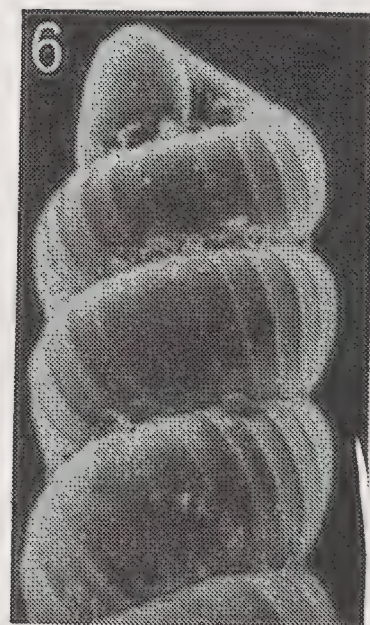
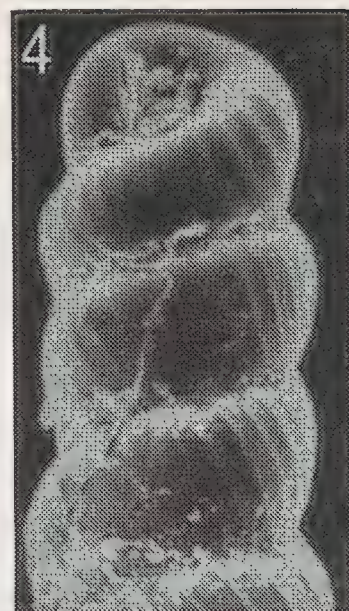
PLATE 2 SHELLS OF *GEOSCALA* AND *SIMPLICERVIX*

- Fig. 1–3. *Simplicervix inornata* (C. B. Adams), paralectotype, MCZ 275693a,  $\times 10$ .  
Figs. 4–11. Apex and nepionic shell in *Geoscala* and *Simplicervix*.  
Figs. 4–14. Scanning electron micrographs.  
Fig. 4. *Geoscala seminuda* (C. B. Adams), Pusey Hill, Manchester,  $\times 47$ .  
Fig. 5. *Geoscala costulata* (C. B. Adams), Cave River, Clarendon,  $\times 50$ .  
Fig. 6. *Geoscala robertsi* (C. B. Adams) Runaway Grotto, St. Ann,  $\times 47$ .  
Fig. 7. *Simplicervix inornata* (C. B. Adams), Fern Gully, St. Ann,  $\times 50$ .  
Fig. 8. *Geoscala seminuda* (C. B. Adams), Stony Hill, St. Andrew,  $\times 100$ .  
Fig. 9. *Geoscala costulata* (C. B. Adams), Cave River, Clarendon,  $\times 48$ .  
Fig. 10. *Geoscala robertsi* (C. B. Adams), Runaway Grotto, St. Ann,  $\times 53$ .  
Fig. 11. *Simplicervix inornata* (C. B. Adams), Fern Gully, St. Ann,  $\times 62$ .  
Figs. 12–14. Ribbing on *Geoscala* species.  
Fig. 12. *Geoscala seminuda* (C. B. Adams), Pusey Hill, Manchester,  $\times 26$ .  
Fig. 13. *Geoscala costulata* (C. B. Adams), Cave River, Clarendon,  $\times 50$ .  
Fig. 14. *Geoscala robertsi* (C. B. Adams), Runaway Grotto, St.  $\times 50$ .

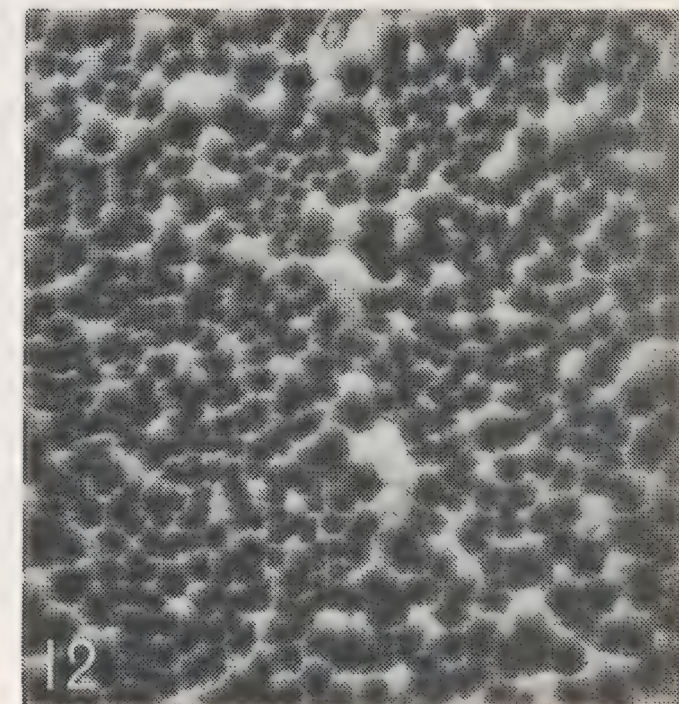
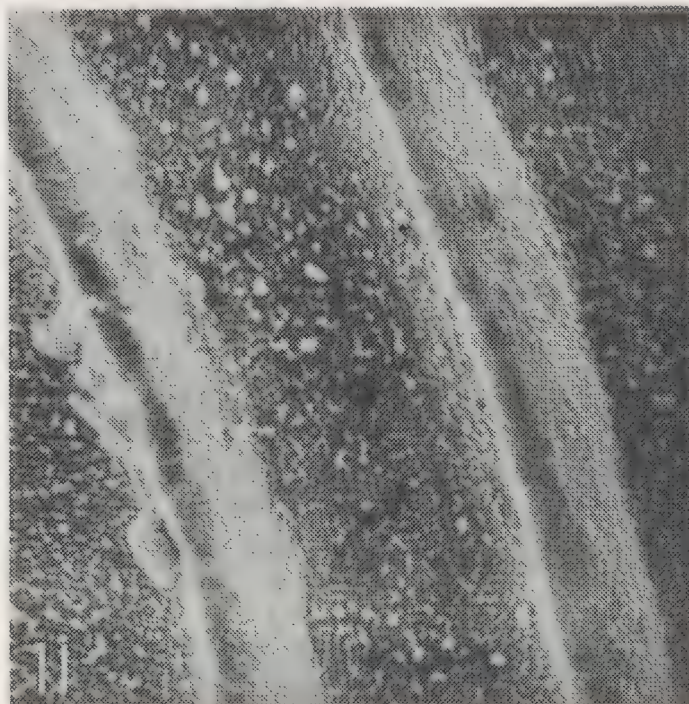
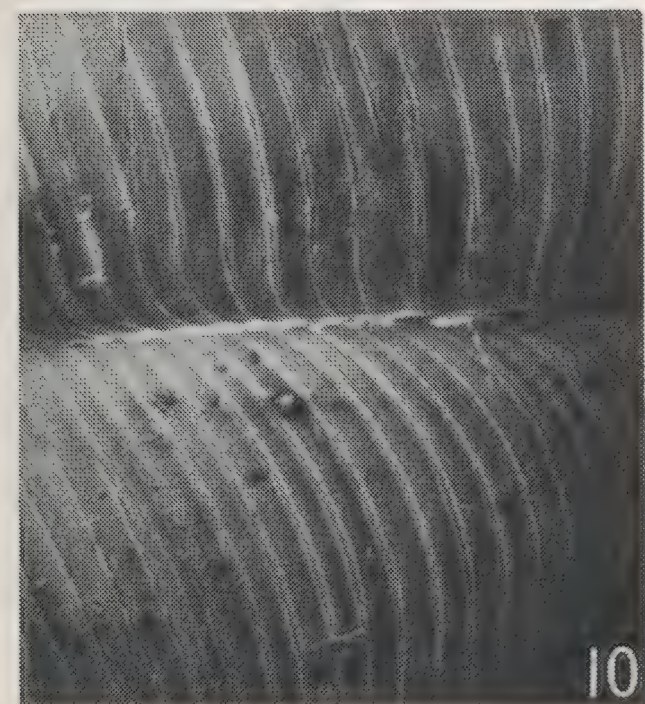
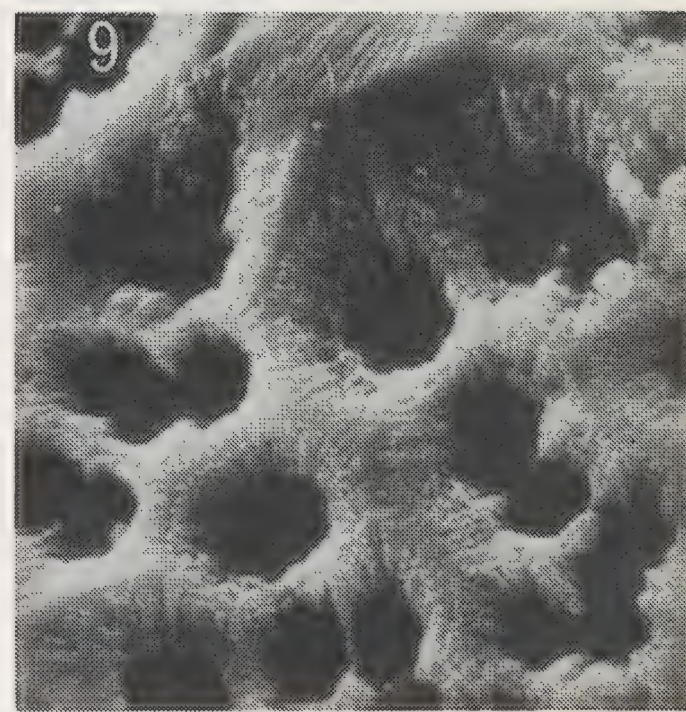
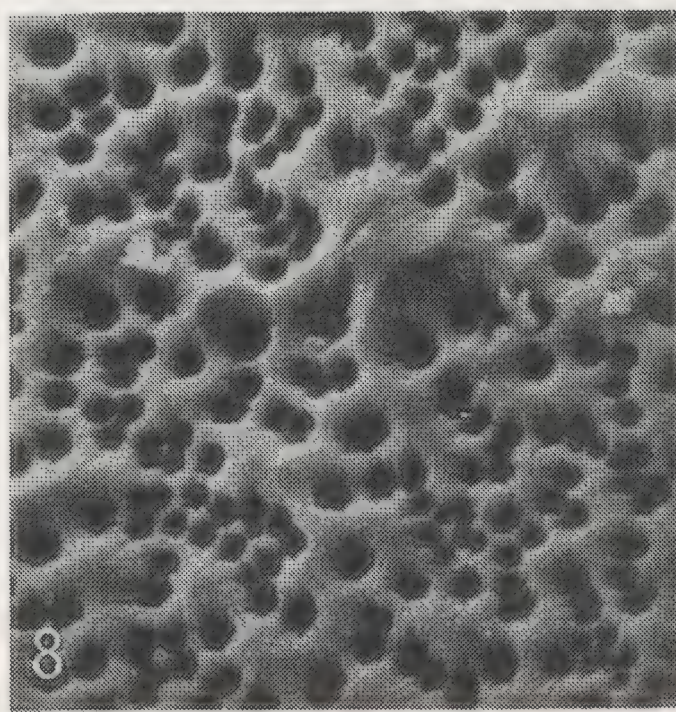
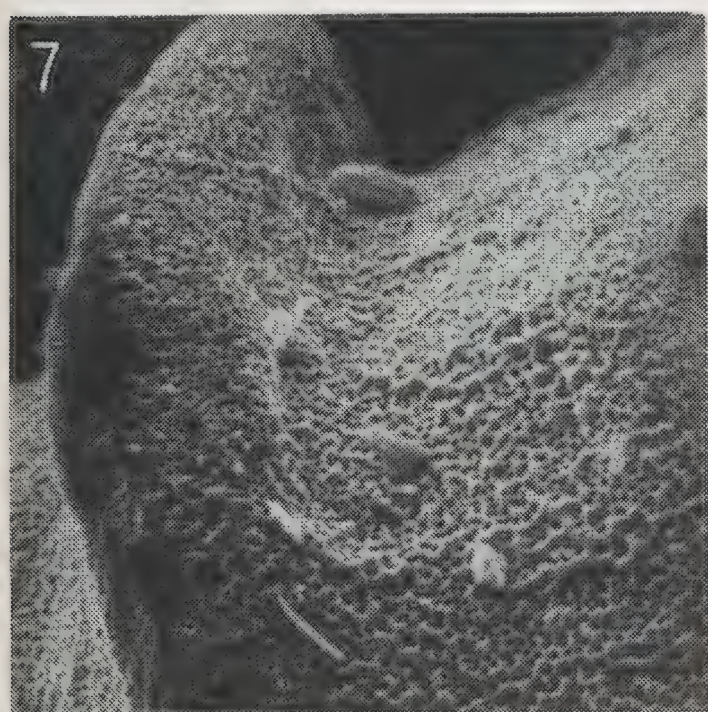
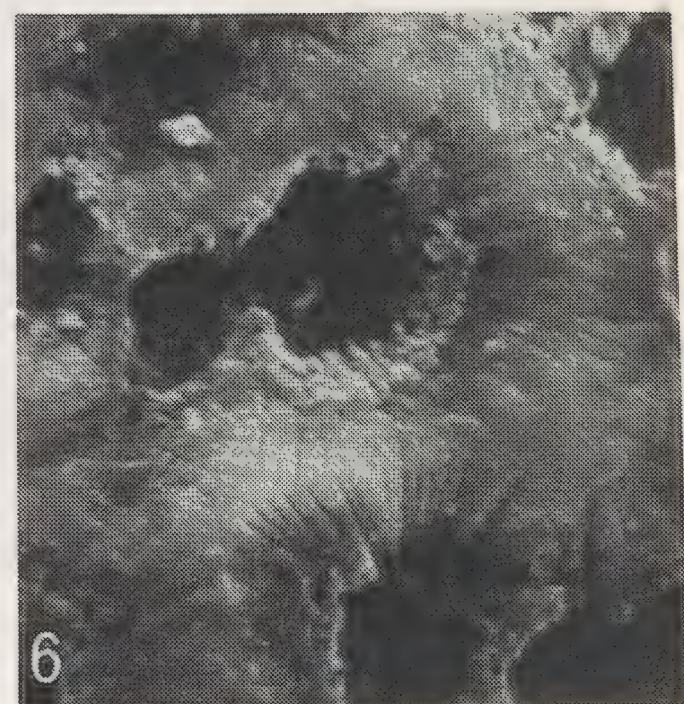
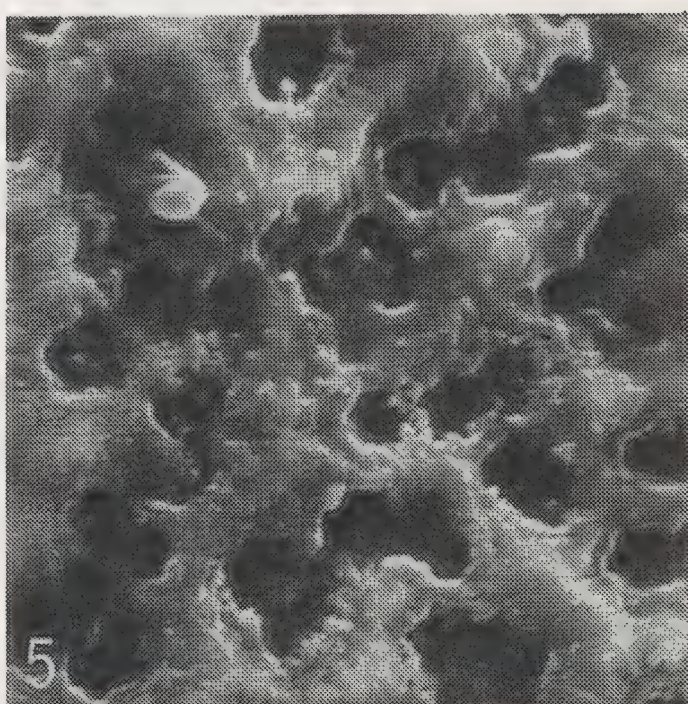
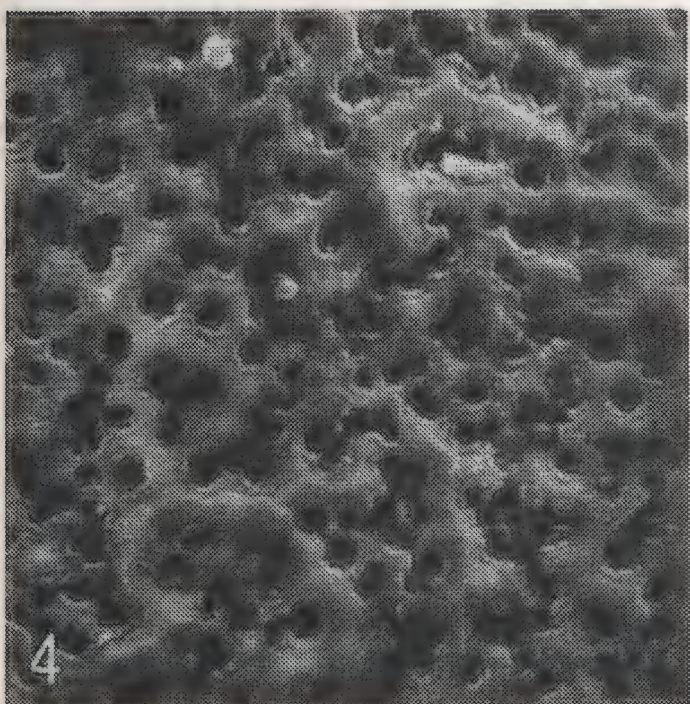
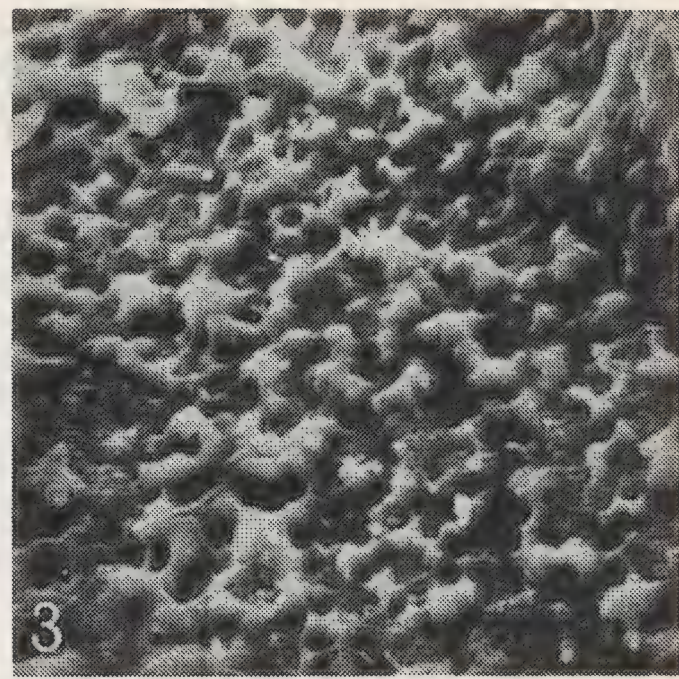
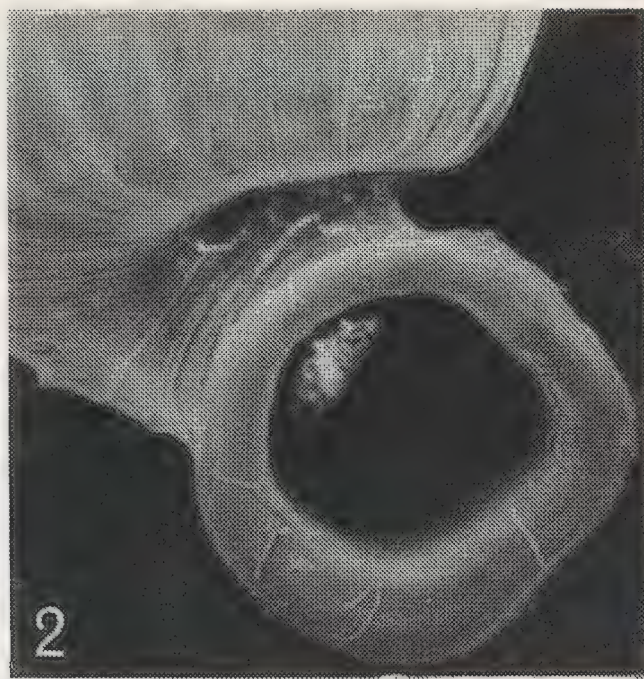














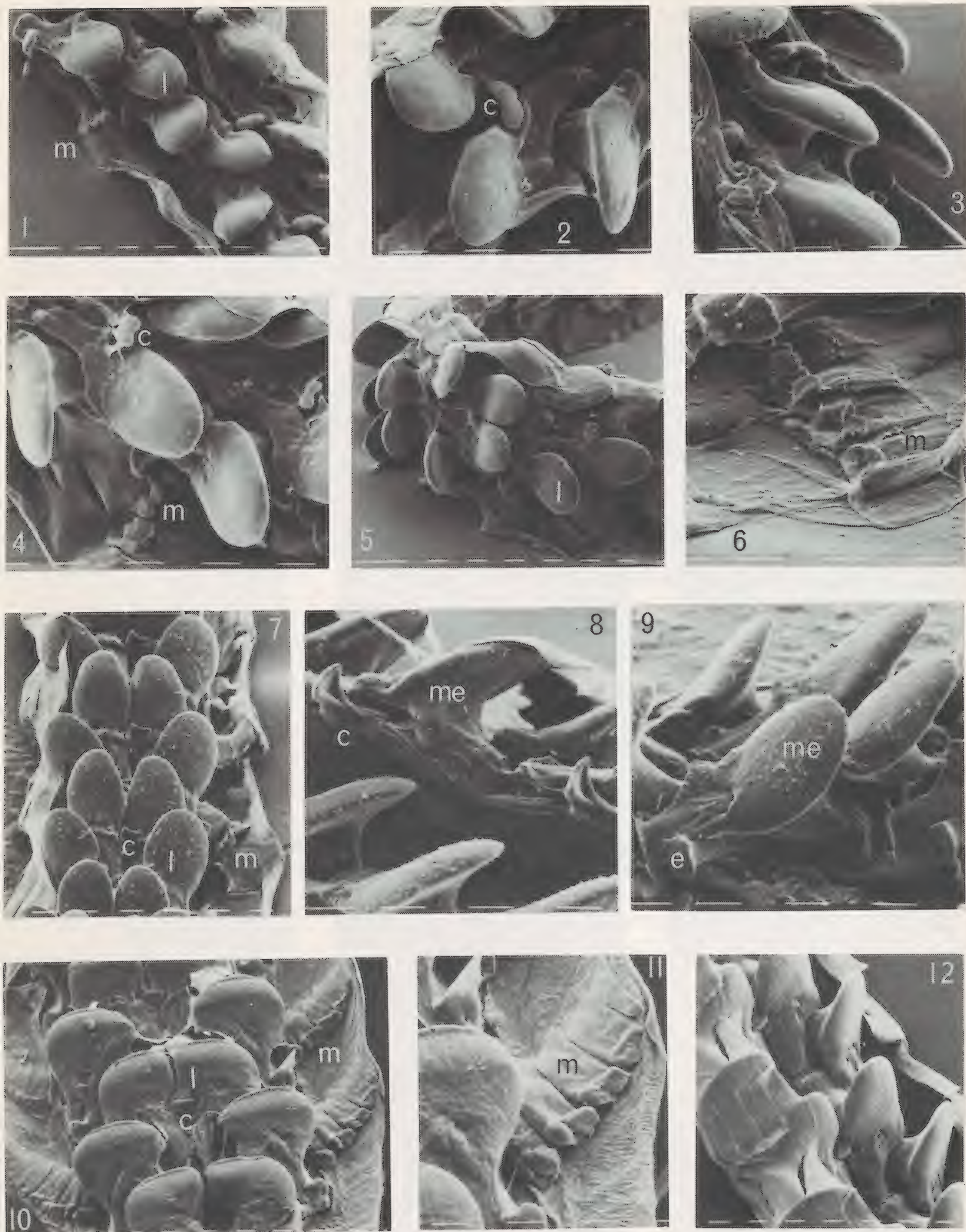


PLATE 4



PLATE 3 PERIOSTRACUM IN *GEOSCALA* AND *SIMPLICERVIX*

Figs. 1–3. *Geoscala costulata* (C. B. Adams), Cave River, Clarendon.

Fig. 1. Uncoiled neck of shell,  $\times 25$ . Fig. 2. Aperture,  $\times 24$ .

Fig. 3. Periostracum,  $\times 965$ .

Figs. 4–6. *Geoscala seminuda* (C. B. Adams), Stony Hill, St. Andrew. Periostracum,  $\times 1000$ ,  $\times 2500$  and  $\times 5050$ .

Figs. 7–9. *Geoscala robertsi* (C. B. Adams), Runaway Grotto, St. Ann. Fig. 7. An individual rib,  $\times 250$ . Figs. 8–9. Periostracum,  $\times 1000$  and  $\times 2500$ .

Figs. 10–12. *Simplicervix inornata* (C. B. Adams), Fern Gully, St. Ann. Figs. 10–11. Ribbing,  $\times 26$  and  $\times 260$ . Fig. 12. Periostracum,  $\times 1050$ .

All figures scanning electron micrographs.

PLATE 4 RADULAR TEETH OF *GEOSCALA* AND *SIMPLICERVIX*

Figs. 1–3. *Geoscala seminuda* (C. B. Adams), Rectory, Manchester.

Fig. 1. General view across radula showing central, large lateral and small marginal teeth. NB ectocone of outer lateral.  $\times 300$ .

Fig. 2. Detail of bilobed central and large laterals.  $\times 600$ .

Fig. 3. Side view showing scraping surfaces of mesocones of lateral teeth.  $\times 600$ .

Figs. 4–5. *Geoscala costulata* (C. B. Adams), Cave River, Clarendon.

Fig. 4. Detail of central, lateral and marginal teeth.  $\times 600$ .

Fig. 5. General view of part of the radula.  $\times 300$ .

Figs. 6–9. *Geoscala robertsi* (C. B. Adams), Runaway Grotto, St. Ann.

Fig. 6. Detail of marginal teeth and ectocone of outer lateral tooth.  $\times 700$ .

Fig. 7. General view of large lateral teeth to show outline which resembles the sole of a shoe and is typical of the mesocones of lateral teeth in *Geoscala* (cf. fig. 10).  $\times 350$ .

Fig. 8. Oblique view of damaged part of the radula revealing complete central tooth and scraping surfaces of lateral teeth.  $\times 700$ .

Fig. 9. Detail of outer lateral tooth showing functional mesocone and almost vestigial ectocone.  $\times 700$ .

Figs. 10–12. *Simplicervix inornata* (C. B. Adams), Mount Horeb, St. James.

Fig. 10. General view across radula showing weakly trilobed central teeth, large lateral teeth and small marginal teeth.  $\times 300$ .

Fig. 11. Detail of five small marginal teeth. NB the outermost has only one cusp.  $\times 600$ .

Fig. 12. Oblique view of lateral teeth.  $\times 300$ .

c central tooth, e ectocone of lateral tooth, l lateral tooth, m marginal tooth, me mesocone of lateral tooth.

All figures scanning electron micrographs; scale bars 10  $\mu\text{m}$  in all figures.







# PROCEEDINGS OF THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

## REPORT OF THE COUNCIL 1981–1982

It is with regret that the Society has to report the deaths of Miss M. A. Cobley and Mr. L. W. Hill, who both joined the Society in 1973, and Mr. F. E. B. Johnson who joined in 1968.

During 1981 the Council of the Society decided to confer Honorary membership on Mr. S. P. Dance and Mrs. E. B. Rands in recognition of the many services they have given to the Society.

Total membership now stands at 626 and is comprised of the following categories:— Full Members 515, Full Life Members 36, Family Members 31, Family Life Members 7, Honorary Members 5, Junior Members 31, Total, 625.

*Resignations:* Full Members 23, Junior Members 1, Total, 24.

*Struck off for non payment of subscription:* Full Members 27, Junior Members 2, Total, 29.

*New members elected during 1981/2:* Full Members 54, Junior Members 10, Total, 64.

### *Meetings*

There were 7 ordinary meetings and one Special General Meeting held, in addition to the Annual General Meeting. The ordinary meeting held on February 20th 1982 was a very successful joint meeting with the Malacological Society of London.

### *Publications*

Two parts of the *Journal of Conchology* were issued, Volume 30 parts 5 & 6. Four issues of *The Conchologist's Newsletter* were printed & issued with the Annual Programme card of events. An up dated list of changes in the membership was issued instead of the usual full list of members. This was an economy measure in view of the high cost of printing. Papers for Students No. 18, *How to collect Marine Mollusca (including so-called rare species)*, by Shelagh M. Smith, was published in December.

### *Change of officer*

Mrs. E. B. Rands will be retiring from the post of Honorary Secretary, having served in that capacity since December 1971. She will be succeeded by Miss J. D. Nunn at the end of May 1982. Council wish to take this opportunity of thanking Mrs. Rands for her work on behalf of the Society.

*Field Meetings 1981:* Nine field meetings were held during 1981 as follows:— May 9th. Camber Sands, East Sussex. June 6th. Grand Union Canal. June 13th.–14th. Hackness, Yorks (joint meeting with the Yorkshire Conchological Society). June 28th. Flitwick Moor, Beds. July 11th. West Runton, Norfolk. July 26th. Joint meeting with the Northampton N.H.S. Sept. 12th. Pashford Pens, Suffolk. Sept. 19th.–20th. Rhossili, Gower. Oct. 18th. Midhurst, West Sussex.

Thanks are due to the following for leading these meetings:— Mr. A. P. H. Oliver, Mr. I. M. Evans, Dr. J. H. Mathias, Mr. A. Norris, Dr. B. Verdcourt, Mr. P. G. Cambridge, Mr. G. Osborn, Mr. E. Milne-Redhead, Dr. P. Graham Oliver and Mr. M. J. Willing.

## TREASURER'S REPORT, 1981

I am happy to be able to report that the Society's balance sheet for 1981 shows a slight surplus of income over expenditure. The amount corresponds almost exactly to the saving made by not issuing a Members' List, since the cost of the 1980 list was £503.32 compared with the cost of £122.53 for the list of alterations issued in 1981.

Obviously this is a very narrow margin, and with the increase in postal charges already in operation, and with probable increases in the cost of printing, it was prudent to raise the subscription for 1982.

Most of the items shown in the accounts are similar to those for 1980, except for the cost of the Special Publication which appeared in that year. Members' and Subscribers' subscriptions show a slight increase. There is a slight decrease in the investment income, due to the fact that it was not possible to retain such a large balance in the deposit account.



THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND  
INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31st DECEMBER, 1981

	£	£	£
Publications:—			
News Letter .....	1,747.33		3,717.51
Student Papers .....	109.79		1,863.64
			33.00
			<hr/>
Journals:-			5,614.15
Volume 30 No. 5 .....	2,446.43		
Volume 30 No. 6 .....	1,824.28		
	<hr/>		119.77
	4,270.71		
Cost of Atlas, Postage and Packing Printing, Stationery and Postage .. Officers' Expenses .....	29.10 578.99 308.29	Sales:— Atlas .....	92.24 11.70 62.14
Subscriptions .....	7.00	Journals .....	90.82
Meetings .....	152.50	Student Papers .....	16.11
Book Markers .....	43.13	News Letter .....	25.92
Sundry Expenses .....	7.50	Book Markers .....	36.40
		Sundries .....	<hr/>
			335.33
			101.00
Net Surplus .....	<hr/>	Special Publication .....	
	7,254.34		
	360.26		
	<hr/>		
	£7,614.60	Investment Income:—	
	<hr/>	General Account .....	1,018.85
		Life Members Fund .....	425.50
		Reserve and Research Fund .....	229.91
			<hr/>
			1,674.26
		Transfer to Reserve and Research Fund .....	229.91
			<hr/>
			1,444.35
			<hr/>
			£7,614.60



BALANCE SHEET AS AT 31st DECEMBER, 1980

Creditors and Accrued Charges ....	£		£	
Fees and Subscriptions in Advance		2,429.96	Cash at Bank:—	
Life Membership Fund .....		798.02	Current Account .....	1,428.34
Reserve and Research Fund .....		2,890.00	Deposit Account .....	2,024.61
<i>Capital Account</i>		1,791.41	Post Office Savings Bank .....	3,759.91
Balance Brought Forward .....	6,919.99			<u>7,212.86</u>
Add Surplus for the Year .....	<u>360.26</u>		Investments:—	
		7,280.25	£400 5% Treasury Stock 1986/89	344.00
			£500 5¾% Debenture Stock—Mersey	
			Docks & Harbour Board 1980/82	222.29
			2514 Units M. & G. Dividend Fund	1,522.06
			£400 12½% Loan City of Norwich	400.00
			£800 5½% Loan London County	
			Council .....	769.20
			1620 Save and Prosper Units .....	892.95
			£875 Spillers 7% Debenture Stock	
			1978/83 .....	753.82
			£700 Bury 12¼% Loan .....	700.00
			£800 15½% Treasury Stock 1998	768.00
			£95.68 Subordinated Loan Stock—	
			Mersey Docks and Harbour Board	95.68
			104 10p Ordinary Shares—Mersey	
			Docks & Harbour Board	10.40
			£2340 7¼% Whitbread Stock 1995/99	1,498.38
		<u>£15,189.64</u>		<u>7,976.78</u>
				<u>£15,189.64</u>

L. LLOYD-EVANS } *Hon. Auditors*  
C. W. PETTITT }

MARJORIE FOGAN  
*Hon. Treasurer*

24th February, 1982



20 Ordinary Members and 6 Junior Members are in arrears with 1981 subscriptions. No further publications can be sent in 1982 to any Member whose current subscription remains unpaid, although these will be sent on receipt of arrears.

Many Members failed to amend their bankers' orders. All Members paying by banker's order are asked to check that those were for the correct amount and to forward any sum outstanding so that the expense of reminders may be avoided. (If the order did not reach the bank before 1.1.82 the bank will not pay on it until January 1983.)

MARJORIE FOGAN, Hon. Treasurer.

## RECORDER'S REPORT: NON-MARINE MOLLUSCA

### A. Grid mapping

A second edition of the *Atlas of non-marine Mollusca of the British Isles* is becoming increasingly desirable. Since 1976 further species have been recognized and mapping coverage has also improved considerably. Nevertheless, some surprisingly large tracts of these islands are still virtually unknown from the molluscan point of view: there are no modern data for 167 10-kilometre squares in Ireland and for 147 squares in Great Britain (see map). Squares with fewer than fifteen species must also in most cases be regarded as badly under-recorded. The most serious lacuna of all remains a large area of potentially rich molluscan territory in north-central Ireland, covering parts of Meath, Longford, Cavan, Louth, Monaghan, Fermanagh and Armagh. Much of Scotland north of the midland valley is also poorly known. Conversely, in England and Wales mapping coverage is now moderate to excellent—though even here some counties could do with closer attention, the most obvious being Devon (v.c.'s 3 and 4), Cardigan (v.c. 46) and Nottingham (v.c. 56).

May I urge members to do all they can to try and close these gaps in time for a second edition of the *Atlas*, which I hope can be published not later than 1984.

### B. Vice-county records

This year has seen the publication of a new Census (*J. Conch., Lond.* **31**: 63) incorporating all vice-comital records published since the last edition in 1951 (*J. Conch., Lond.* **23**: 171). During its compilation a certain number of further verified records came to light which, for one reason or another, have never appeared in print. However, the majority of these are of common or otherwise unremarkable species and there therefore seems little point in including them in the list below, which, as has been usual in recent years, is concerned only with increments made during the 1981–2 season; common segregates (e.g. of *Arion*) have also been omitted.

\*Not included in the 8th edition of the Census.

Somerset North (6): *Boettgerilla pallens*, Midsomer Norton (31/6454), M. J. Willing.

Isle of Wight (10): *Boettgerilla pallens*, Shorwell (40/4583), Mrs. E. B. Rands.

Surrey (17): \**Cochlicella acuta*, Pewley Down, Guildford (51/0049), M. O. Moss.

Essex South (18): *Limax flavus*, Westcliff on Sea (51/8686), J. F. Skinner.

Suffolk East (25): *Marstoniopsis scholtzi*, R. Deben, Rendlesham (62/3253); *Milax gagates*, Kesgrave (62/2345);

\**Deroceras caruanae*, Levington (62/2339), I. J. Killeen.

Bedford (30): *Boettgerilla pallens*, Flitwick (52/0434), D. Guntrip and Mrs. E. B. Rands.

Lancaster West (60): *Vertigo angustior*, Gait Barrows NNR, Silverdale (34/4877), Mrs. D. K. Marriott.

York South-west (63): *Ferrissia wautieri*, canal between Brighouse and Elland (44/1323), A. Norris.

Perth East (89): *Vertigo alpestris*, Creag an Duibh, Glen Tilt (27/9878), Mrs. D. K. Marriott.

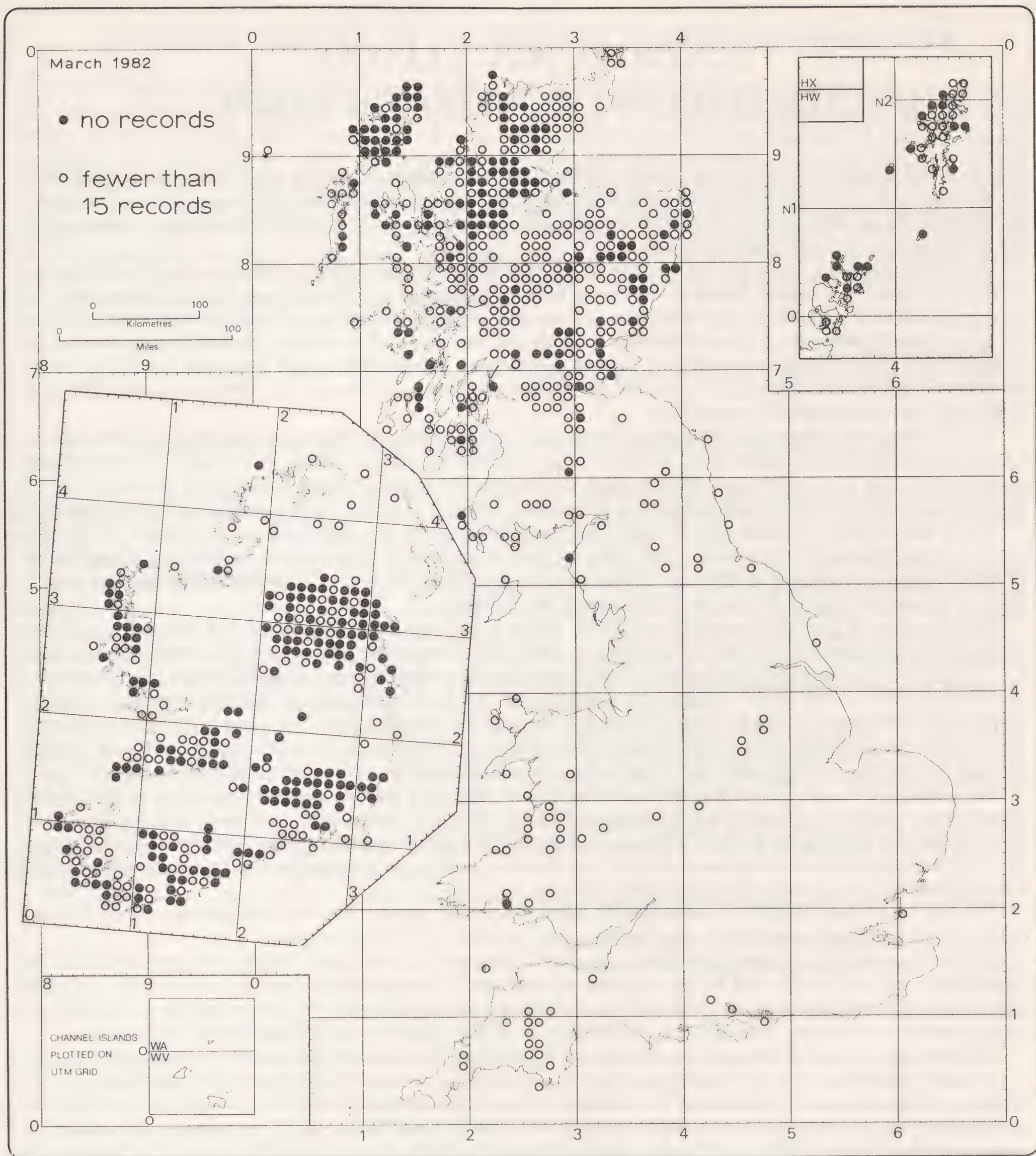
Dublin (H 21): *Spermodea lamellata*, Luttrellstown (32/0537), R. Anderson; \**Limax valentianus*, Carrick Hill Road, Portmarnock (32/24; garden), D. Doogue.

The outstanding discovery of the year has been that of the extremely rare *Vertigo angustior* in Lancashire (see also *J. Conch., Lond.* **31**: 72). The habitat is an unusual one—a damp limestone pavement. Also noteworthy is *Vertigo alpestris* from a limestone scree in Glen Tilt, the first known site for this species on the Scottish mainland (*J. Conch., Lond.* **31**: 135).

Among freshwater molluscs an important find has been *Marstoniopsis scholtzi* in the R. Deben in Suffolk. This follows on a discovery in the Norfolk Ouse in 1978 (*J. Conch., Lond.* **30**: 135). *Ferrissia wautieri* from Yorkshire represents a significant extension to the known range of a species first noted in Britain only in 1976.

Among the slugs, *Boettgerilla pallens* has been found in three more vice-counties, making 22 since its first recognition in Britain ten years ago. *Limax (Lehmannia) valentianus* has been found living in the open in a suburban garden at Portmarnock in Co. Dublin, and also at the edge of a nearby coastal saltmarsh. This south-west European slug was previously known in the British Isles only in greenhouses, in London (Kew), Swansea and Belfast. It will be interesting to see whether the species becomes truly naturalized in these islands.





A large thriving colony of *Cochlicella acuta* was found in chalk grassland at Guildford, no doubt introduced. Like other similar inland colonies noted from time to time (e.g. in Wiltshire (1929), Suffolk (1933) and West Kent (1934)) it is unlikely to survive the first really cold winter.

M. P. KERNEY

#### RECORDER'S REPORT: MARINE MOLLUSCA

At the time of writing (May 1982), the Nature Conservancy Council is printing the *Sea Area Atlas Of Marine Molluscs of Britain and Ireland* for the Society, and it should be available during the summer.

In future years I will give details in this annual report to enable the atlas to be kept up-to-date with additions and amendments, until such time as a more detailed atlas is produced some years hence.

D. R. SEAWARD



# COMMUNICATIONS

## FISH IN THE DIET OF *DRUPA RICINUS HADARI*

Species of the gastropod genus *Drupa* (family Muricidae) are abundant in shallow wave-swept habitats of Indo-Pacific coral reefs. Although eight species and three subspecies have been described (Emerson, W. & Cernohorsky, W. 1973 *Indo-Pacific Mollusca* 3:801–864), five of these, namely, *Drupa ricinus*, *D. morum*, *D. rubusidaeus*, *D. lobata* and *D. grossularia* are generally the most abundant.

With few exceptions, most members of the family Muricidae feed by drilling shelled prey such as barnacles, bivalves and other gastropods. However, species of *Drupa* feed upon very different types of prey; *Drupa morum* eats eunicid and nereid polychaetes. *D. rubusidaeus* eats eunicid polychaetes and sometimes sponges, whilst the two similar species *D. lobata* and *D. grossularia* both eat sipunculid worms. Of all the species studied *Drupa ricinus* has the broadest diet which includes nereid and eunicid polychaetes, sipunculids, small crustacea (including crabs, amphipods, isopods and barnacles), vermetid gastropods and chitons (Taylor, J. D. 1978 *J. exp. mar. Biol. Ecol.* 31:83–103, and unpublished observations).

*Drupa ricinus* is represented in the Red Sea by an endemic subspecies *D. ricinus hadari* (Emerson & Cernohorsky 1973) which differs from *D. ricinus ricinus* by being larger and heavier, and possessing, in the adult, a well developed parietal shield. On Harvey Reef, an offshore patch reef, part of the Towartit Group 18 km south of Port Sudan, the species is common in shallow rocky habitats on the easterly exposed edge of the reef, reaching densities around 0.9/m<sup>2</sup> and also occurs less commonly on dead coral surfaces all across the patch reef (survey August 1978). The species is also common in similar habitats on other reefs in the area and in other parts of the Red Sea (Mastaller, M. 1979 PhD Thesis, University of Bochum). *Drupa morum* is also abundant in the exposed reef edge habitats and *D. lobata* is occasionally found on the dead upper surfaces of corals.

Identification of the gut contents from 114 *D. ricinus hadari* revealed a diet consisting of crustacea (crabs, stomatopods, amphipods) 57%; nereid polychaetes 17%; eunicid and other polychaetes 4%; vermetid gastropods 11%; chitons 4%; but with eight individuals (7%) containing the scales and bones of small juvenile fish. The fish are estimated to have been around 2 cm in length, and although specific identification of the remains was not possible, they definitely belonged to the Gobiinae. These fish are common inhabitants of holes and crevices in coral reefs. Most of the items in the diet of *Drupa* species inhabit holes and crevices in reef rock and the gastropods catch them by probing into cavities with the extensible proboscis, the entrance to the cavity being covered by the gastropod. Although many of the prey are very mobile animals, it is not clear how immobilisation of the prey is accomplished. *Drupa ricinus hadari* is significantly larger (mean shell height  $26.1 \pm 4.3$  mm,  $n=96$ ), compared with Indian Ocean *Drupa ricinus* (e.g. Aldabra Atoll,  $20.4 \pm 3.0$  mm,  $n=403$ ) and the capture of small crevice-living fish should be within their capabilities and probably no more difficult than catching crabs or errant polychaetes. This is the only record of live fish feeding by a gastropod outside of the Conidae.

The two other *Drupa* species, *D. morum* and *D. lobata* which also occur on Harvey Reef had a diet of eunicid and nereid polychaetes and sipunculids respectively, a diet similar to that of other areas.

As is well known, several species of *Conus* including *G. geographus*, *C. catus*, and *C. tulipa* feed upon fish which are immobilised by a toxin delivered by the dart-like radular teeth. *D. ricinus hadari* does not possess such advanced anatomical adaptations and would not be able to catch free-swimming fish, but only prey which are prevented from escape within rock cavities. Nevertheless, the techniques of prey capture would repay further investigation.

The feeding activities of *Drupa* species are interesting amongst the predatory gastropods, for although belonging to the family Muricidae, they are feeding upon prey types which are the main food of species in other families which are also common in coral reef habitats. For instance, most of the reef-living Mitridae of which the diet has been studied, feed upon sipunculid worms which are the main food of *Drupa lobata* and *D. grossularia*; additionally, *D. morum* and *D. rubusidaeus* feed upon the same species of eunicid polychaete worms which are eaten by *Conus* species (Kohn, A. J. 1968 *Ecology* 49:1046–1061) living in the same habitats.

### ACKNOWLEDGEMENTS

I am grateful to Dr. S. M. Head and the Cambridge Coral Starfish Group for the opportunity of working in Port Sudan and to Mr. G. Howes for examining the fish remains.

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## A FURTHER RECORD OF *CYATHOPOMA AZANIENSE* VERDCOURT

In 1978 I described a minute operculate of the family Cyclophoridae from the Kenya coast based on a single dead shell collected by Strinati and Aellen in 1975. (*Basteria* **42**, p. 15, fig. 1). Working through the large collection made by the arachnologist Åke Holm loaned to me by the Natural History Museum in Stockholm I found two more specimens, live-collected and in spirit, which had been found in litter in a cave at Shimoni 5 years earlier, 13 March 1970, Holm 254. The holotype was also found near the Shimoni Caves. It would be foolish of me to destroy one of these minute shells since its dissection would require an expert; they are left for some serious worker on the family to investigate. The operculum can, however, be described as circular, concave, withdrawn a little way within the aperture of the shell and with a thin raised spiral ridge on the outer face as described for the related species *C. africanum* Pilsbry. Serious investigation of these caves would probably yield much more material which would enable the anatomy to be studied from a number of specimens.

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## *VERTIGO ALPESTRIS* ALDER IN PERTHSHIRE, SCOTLAND

During a survey of the molluscs of a limestone area in Glen Tilt, Perthshire (v.c. 89), a specimen of a *Vertigo* species was collected that on later examination was found to be *Vertigo alpestris* Alder. This is only the second record for Scotland, the other being a 1948 record from Mull (*J. Conch., Lond.* **23**, p. 41).

The site where the single living specimen of *V. alpestris* was found was among scree on a steep west facing slope at an altitude of 400 m (NN 983788). The scree was composed mostly of limestone and had virtually no foliose lichen or moss growing on it, just a film of algae or crustose lichen. Relatively few higher plants grew in the scree, though *Geranium robertianum* L., *Saxifraga oppositifolia* L., *S. aizoides* L., *Rubus idaeus* L. and *Prunella vulgaris* L. were characteristic of the area and occasionally grew in the scree. No further search was carried out for more specimens of *V. alpestris* as it was not distinguished at the time from *V. substriata* which had been found about a kilometre away in a less calcareous site, although the more yellow colour of the shell was noticed.

Twenty-six other species of mollusc were found in the vicinity of the find, though not all in the scree. They included catholic species such as *Nesovitrea hammonis* and *Euconulus fulvus*, and more calcicole species such as *Ena obscura*, *Trichia hispida*, *Arianta arbustorum* and *Cepaea hortensis*. *Columella aspera*, *Discus rotundatus*, *Clausilia bidentata* and *T. hispida* were found living actually in the scree.

The limestone of Glen Tilt is only part of a band of calcareous strata running from Schiehallion in Perthshire to Tomintoul and beyond in Banffshire. The present find suggests it would be worth looking out for *V. alpestris* in suitable scree habitat in this region of Scotland.

We should like to thank Dr. M. P. Kerney for confirming the identification of the specimen of *V. alpestris*.

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## **EIGHTH INTERNATIONAL MALACOLOGICAL CONGRESS**

The Eighth International Malacological Congress, sponsored by the Unitas Malacologica, will be held in Budapest, Hungary, in 1983, in the period August 29–September 3. Further information can be obtained by writing to László Pintér, Natural History Museum, Baross u. 13, H-1088 Budapest, Hungary.











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WOODWARD, F. R. 1965. Monograph of the British Lower Tertiary Unionidae, with descriptions of three new species. *J. Conch., Lond.* **25**: 316–330, pls. 22–27.

GOULD, S. J. 1969. An evolutionary microcosm: Pleistocene and Recent history of the land snail. *P. (Poecilozonites)* in Bermuda. *Bull. Mus. comp. Zool. Harv.* **138**: 407–532, 5 pls.

8. Authors may obtain copies of all papers at cost price if ordered from the printers, via the Hon. Editor, when the galley proofs are returned.



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# CORNISH MARINE CONCHOLOGY

STELLA M. TURK\*

*(Presidential address, delivered before the Society at the British Museum, Natural History, 20 March 1982)*

## INTRODUCTION

Cornwall's long coastline, with its varied topography and geology, would lead one to expect a diversified fauna and flora. Add to this the extreme south-westerly position of Cornwall and the Isles of Scilly, in the path of the North Atlantic Drift with consequent mildness of climate, and this anticipation is abundantly realised. A number of Mediterranean and other warm-water species reach their northern limits on Cornish and Scillonian coasts, and evidence indicates that these do not have a steady state, but fluctuate according to long-term cyclic changes such as are believed to take place in the Channel. Molluscs provide particularly valuable clues to such changes, as shells may remain to show past distribution. The far South-West has attracted conchologists to its shores for over two centuries, and Cornish specimens have found their way into major and minor collections throughout the British Isles. With this background, both its study and the history of its study are complex. The fact that it continues to be a popular holiday, retirement and research area, increases the pressures on its shores and shallow seas, especially the sheltered marine inlets, and underlines the need for marine conservation measures and careful monitoring.

## BRIEF HISTORY OF THE STUDY OF CORNISH MARINE MOLLUSCA

Many of our more well-known resident naturalists, some of whom retired here, were interested in varying degrees in molluscs and published lists of them and notes about them. The majority of such residents, mainly clergymen, doctors and teachers in the 18th and 19th centuries, were essentially communicators and centralisers of records, sending information to other naturalists at home and abroad, and in turn receiving some specialist help. Much is also owed to those visitors who studied or collected in Cornwall, during long or short stays, often intent on comparing the Cornish and Scillonian molluscan fauna with that of northerly collecting stations in the British Isles, so sampling the extreme faunal elements. The Channel Isles have attracted similar attention over the decades for their southern species, but although politically linked with Britain, it is part of the French region in biogeographical terms. The existence of the Royal Institution (founded 1818), the Royal Cornwall Polytechnic Society (1833), the Penzance Antiquarian and Natural History Society (1839-1960) and the Royal Geological Society of Cornwall (1814) all contributed to the widespread study of molluscs, Recent, sub-fossil and fossil, in the 19th century, by encouraging the publication of records and by having museums which welcomed collections. The Royal Institution of Cornwall offered £10 for the best essay on Cornish conchology in the years 1838-1841, and the Royal Cornwall Polytechnic Society gave annual awards for over a century for various natural history projects, including conchological ones. The publication of the *Victoria History of Cornwall* enabled all these records and lists of marine molluscs to be summarised (Clark 1906). Since 1884, the focal point of marine research has been provided for much of the British Isles and overseas, by the Marine Biological Association of the United Kingdom, and the siting of the laboratory at Plymouth in 1888 has ensured that the fauna

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and flora of Devon and much of Cornwall has been extensively studied within the widest context of oceanographical factors. The south-east of the county received most attention up to the publication of the 3rd edition of the *Plymouth marine fauna* (Marine Biological Association 1957) but active interest in the whole Cornish marine scene has been intensified by two major events: the opening of the Tamar Bridge to road traffic in October 1961, making Cornwall more readily accessible, and the wreck of the 'Torrey Canyon' on the Seven Stones reef in March 1967 (Smith 1968) with a consequent massive oil spillage which emphasised how little we knew about individual sites on and off the Cornish coast. Research in the Tamar and Lynher estuaries has greatly increased since the establishment of IMER (Institute of Marine Environmental Research, Natural Environment Research Council) at Plymouth in 1974. The revival of the Conchological Society's Marine Census Survey in 1961 has also done much to increase our knowledge of the distribution of molluscs in Cornwall, as in other parts of Great Britain and Ireland: the publication of Sea Area lists (Seaward 1979) has now been followed by the Sea Area Atlas (Seaward 1982). The work has been aided by the fast-growing interest in diving and marine conservation, fostered by the Federation of British Sub-Aqua Clubs and the Underwater Conservation Society; Porcupine, a group concerned with the recording and ecology of all marine phyla, is also very active, and all three bodies have been concerned with Cornish recording. On a purely Cornubian level, the Cornish Biological Records Unit under the aegis of the Board of Cornish Studies (University of Exeter in collaboration with Cornwall County Council) is providing an impetus for recording and the means for storing all Cornish biological data.

#### ASPECTS OF GEOGRAPHICAL AND ECOLOGICAL DISTRIBUTION

Jeffreys (1862) described the British and mainland European molluscan fauna as having 'northern', 'southern' and 'oceanic' elements, this last being composed of occasional visitors such as violet sea-snails *Janthina* spp. which are particularly frequent off Cornish coasts in some years owing to the strategic position of Cornwall in the path of warm currents of the North Atlantic Drift. He considered that there were no sharp divisions between such faunas, even with only these three categories as compared with the several used by most conchologists of his time. The Western English Channel is an important meeting-place for southern and northern species: Harvey (1969b) writes 'Southern warm-water forms are often commoner here than anywhere else in Britain, while many of the cold-water forms common on other parts of the coasts are often much sparser and are close to their southern limits.' All too little is known of natural fluctuations, but it is as well constantly to remind oneself that life will not easily be strait-jacketed into systems or described in simple statements: it is plastic, protean and prodigiously productive. Verwey (1949) points out that where lower marine forms are concerned, we falsely start from the environment and its pressures, and not from the creature itself as we would with the higher animals. In this way we view the mollusc as if it were 'suspended by invisible threads, spun by light, temperature, salinity etc.', forgetting its own internal 'ecology' and the adjustments which bring about its essential but varying homeostasis. The following are the main factors which help to explain the variations in such a molluscan fauna as that of Cornwall.

1. The potential geographical range of a species may not be realised because the right combination of ecological conditions is absent. Substrate, degree of shelter or exposure, tidal scour, chemistry, turbidity, salinity and temperature are some of the more important factors. The temperature of the air as well as the sea may be critical for littoral and shallow water animals, and of great significance is the difference between summer and winter temperatures, and whether seasonal thermoclines are present. The complex distribution



patterns of many species, including molluscs (mainly bivalves) on both sides and at both ends of the English Channel are discussed in great detail by Holme (1961, 1966), and the varying effects of the above factors on selected species are clearly demonstrated by the innate differences of the French and English sides, and in the western and eastern basins of the Channel. Species cited as 'Cornubian' by Holme (loc. cit.) are such southern types as the venerid *Callista chione* (L.): these have a limited penetration into the Channel, although the high summer temperature of the eastern as compared with the western half, enables certain warm-water species like the dwarf dog-whelk *Nassarius pygmaeus* (Lamarck) the tusk-shell *Dentalium vulgare* (da Costa) and the venerid *Venus verrucosa* L. to be commoner in the Isle of Wight area than on the Cornish coast. By contrast, the temperature stratification of the Outer Western Channel allows a few cold-water species such as *Astarte sulcata* (da Costa) to live off the south coast of Cornwall in deep water. Various limiting factors in the east basin result in fewer species, but more individuals being present; in the western basin there is great species-diversity but fewer individuals.

2. Distribution and the available means of dispersal are closely linked. The dispersal of planktonic larvae is affected by currents and winds, and those with long larval lives may be carried far from their source. Residual water-movements in the Channel are set eastwards, coinciding somewhat with the prevailing south-westerly winds, and it has been suggested by Crisp & Southward (1958) that this may explain the absence from the Isles of Scilly of the warm-water limpet *Patella depressa* Pennant, the scarcity of the mussel *Mytilus edulis* agg. and the great rarity of the common periwinkle *Littorina littorea* (L.). Harvey (1969a) draws attention to the absence of land or shallow water to the west of the Scillies from which replenishments could be expected in the plankton of these mainly littoral species, although he adds that Rennel's current, believed on occasion to set a northerly course from the Ushant to the Isles, could presumably transport these and other larvae from Brittany. It may well be significant that the common periwinkle has a larval life of four to seven weeks, whilst the warm-water trochid *Monodonta lineata* (da Costa) swims freely for only four days: the latter species, abundant in the Scillies, is called a winkle by the Scillonians and takes the place of the winkle in their meals as well as on the rocks.
3. The Channel has been studied almost continuously since the turn of the century by scientists of the Marine Biological Association of the United Kingdom, and there is growing evidence of long-term cyclic changes that operate in the western English Channel, involving fundamental changes in the fauna and flora. Southward (1980) cogently discusses these apparently cyclic phenomena, postulating that there may be a connection with sun-spot activity, and showing that changes are broadly relatable to climatic shifts, with temperature, water-movements, chemical constituents, competition and natural fluctuations all playing a part. From 1900 to about 1950, the Channel waters became progressively warmer as part of the general amelioration of climate in the Northern Hemisphere, and the rate of increase reached a peak in the late 1920s and early 1930s: the major biological concomitant was the complete failure of the herring fishery at Plymouth in 1936. From that year until 1964, pilchards and their eggs were common in the plankton, and the associated warmer conditions were notable for the numbers of warm-water fishes and other animals. As the herring is close to its southern limits at the entrance to the Channel, and the pilchard is near its northern limit, the fortunes of this north/south pair of species are very significant biologically, quite apart from the economic implications. Amongst the Mollusca, it may be relevant that the only living British specimens of the Mediterranean species *Divaricella divaricata* (L.) were found in 1949 and 1950, when sea temperatures were near their maximum, in the Isles of Scilly (Fowler 1949, 1950 & 1952). Although in the 30 years or so prior to 1964, waters were only about



0.5°C. warmer than they have averaged since 1964 (Southward 1980), this is the usual difference between western Channel British coasts and those of the coast of Brittany (Crisp & Southward 1958) where many more southern species continue to survive. With the colder conditions of the past 20 years, many southern species of the fauna and flora have disappeared from our coasts or been pushed back westwards and southwards towards Cornwall and the Isles of Scilly, reversing the trend recorded by Southward & Crisp (1954) who discuss the retreat of the cold-water barnacle *Balanus balanoides* L. and the advance northwards and eastwards of its counterparts, *Chthamalus stellatus* agg.

4. Weather in a single season may favour or decimate a species. Temperature is often of paramount importance in determining success or failure, particularly for reproduction as Wyatt (1961) has shown for *Calyptrea chinensis* (L.), and low winter temperatures are in general more of a check on distribution than high summer ones (Crisp & Southward 1958). One severe winter may check the advance of such southern species as the trochids *Monodonta lineata* and *Gibbula umbilicalis* (da Costa) as likewise the limpet *Patella depressa*, after a series of mild winters has enabled them to increase their range eastwards and northwards. Crisp & Southward (1964) record the effects of the extremely cold winter of 1962/63 on various marine animals, including a number of molluscs, bivalves as well as gastropods, and Hawthorne (1965) describes in detail the fluctuations of *Monodonta*. Some southern species which are at their northern limits in S.W. Britain, probably only breed in the warmest summers, and their continuous presence is therefore due to the fact that they are very long-lived: it has been suggested that the venerid *Callista chione* (L.) may live for at least 40 years (Forster 1981) and it is reasonable to suppose that the large scarce southern cockles *Acanthocardia aculeata* (L.) and *A. tuberculata* (L.) are equally long-lived. Certainly juveniles of all three of these species are decidedly rare in Britain.
5. Any one species may naturally extend its range by increasing its tolerance of previously limiting conditions, or by population explosions elsewhere, the latter being well-demonstrated by the enormous numbers of *Octopus vulgaris* Lamarck that occasionally invade the south coast of England from northern France following a vast increase in numbers (Garstang 1900, Rees & Lumby 1954). They have been described as plagues and their migrations are believed to be due to exhaustion of food supplies.
6. Natural predator/prey fluctuations presumably exist in marine as in non-marine species e.g. ladybirds and aphids. The enormous numbers of the common starfish *Asterias rubens* L. which sometimes occur in between tide-marks, may bear some relationship to availability of their main prey, mussels and scallops.
7. Breeding migrations to shallower water may result in large numbers of certain molluscs congregating on the shore or on shallow water. *Aplysia punctata* Cuvier and *Aeolidia papillosa* (L.) for instance, are in great abundance in some spring seasons. The large whelk *Buccinum undatum* L. comes inshore to spawn throughout the winter months, and the mud can be seen heaving with them in such sheltered sites as Helford Estuary and the Fal Estuary. The occasional vast aggregations of the common periwinkle, *Littorina littorea* seem to be unexplained (Fretter and Graham 1980). In Cornwall I have seen them in heaps, inches deep.
8. Continuous south-westerly winds over a period, bring warm-water oceanic species close to the west coasts of Britain and Ireland, occasionally resulting in massive wrecks of violet sea-snails *Janthina janthina* (L.), *J. pallida* Thompson and, very much more rarely, *J. exigua* Lamarck. All three species have been cast up with the animals still alive but only shells have been found of the cephalopod *Spirula spirula* (L.) which occurs from time to time on western shores of Britain. All of these are probably more frequently found on Cornish



shores than elsewhere. The only British record of the circum-tropical nudibranch, *Fiona pinnata* (Eschscholtz) a member of the fouling community, is from Falmouth, Cornwall, and also from Falmouth are the only drift records of the oceanic species *Scyllaea pelagica* L.: the Plymouth record of *Scyllaea* in 1919, was from the bottom of a sailing ship. Material drifting on the sea surface has been found to travel at 3·3% of the wind speed (Smith 1968), a fact which makes general predictions possible concerning plankton as well as oil slicks.

9. The ecological balance may be affected by naturalised aliens, such as the American slipper-limpet, *Crepidula fornicata* (L.) and the Australian barnacle, *Elminius modestus* Darwin. Several species of algae have been introduced, but none pose the same threat as Japweed, *Sargassum muticum* Yendo, expected to establish itself on certain of the Cornish shores within the next year or two.

#### GENERAL FEATURES AND HABITATS OF THE SHORES AND SHALLOW SEAS OF CORNWALL AND THE ISLES OF SCILLY

Cornwall, the south-west tip of Britain, is noted for its mildness. Revesz (1969, pp. 43–65) gives the average number of days of frost at Plymouth as 27·8, Falmouth, 14·6 and the Isles of Scilly, 3·9. It has been suggested by Harvey (1969a) that the phenomenon of ‘submergence’ discussed by Holme (1961), concerning the way some animals and plants inhabit deeper water in the colder parts of their range although they occur intertidally in the south, may be due to them not being culled by frost in our milder climate. ‘Submergence’ or rather ‘emergence’ is particularly noticeable, not unexpectedly, in west Cornwall and the Isles of Scilly. Low water is around midday and midnight in both Devon and Cornwall: this means that all organisms are exposed to the extreme heat of summer days and the cold of winter nights. Prevailing winds are south-westerly, and the tidal range is between 4 and 6 m. Cornwall has the longest coastline of any English county, stretching 400 miles including the indentations of the estuaries which account for 150 miles. The crenulate nature of the Cornish coastline is especially mentioned by King (1959) as an example of differential resistance to erosion. General descriptions of the Cornish and Scillonian coast appear in SMBA/MBA UK (1978) and Turk (1971a).

#### THE SOUTH COAST: FROM THE PLYMOUTH AREA TO LAND’S END

From the Plymouth area, taken as the Cornish half of the Tamar, to the Land’s End, the coast is very indented and consists mainly of sedimentary Devonian rocks, exceptions being the Lizard peninsula, with its complex geology including its famous serpentine, and the Land’s End peninsula dominated by granite. The Tamar, Fowey and Fal rivers as well as the complex creeks of the Helford, flow in drowned valleys with typical estuary conditions in the upper reaches, and almost fully saline conditions near the mouths: these marine inlets or rias, are extremely important for the richness and diversity of their marine fauna and flora, especially molluscs which are present in large numbers in the soft substrates. Oaks line the valleys, particularly in the Fal and Helford estuaries, their lower branches often festooned with high-tide seaweed drift; the reefs which are generally narrow, show ‘text-book’ zoning. Such sheltered inlets as these are restricted in England to Devon and Cornwall. For their marine life, Helford estuary and the smaller area near St Mawes in the Fal estuary, rank with Salcombe, Devon, in importance. Helford has been described as a sheltered arm of the sea, and over 250 species of Mollusca have been recorded, more than 130 of them found living since 1950. Descriptions of this locality appear in Gardiner (1927), Turk (1976), Turk and



Turk (1976) and SMBA/MBA UK (1978). On the open coast, again with the exceptions of the Lizard area and some of the headlands, the cliffs are mostly low, sloping down to wide reefs often with numerous rock pools and beaches of coarse sand and pebbles: the variations, however, are considerable, the number and size of pools and to presence of boulders and cobbles depending on the geological formations. Off shore from the Tamar to St Austell Bay 'The bottom is patchy with rock, gravel or shale in places, patches of fine sand occurring in Whitsand (and Bigbury) Bays' (Holme 1961). The Eddystone shell gravels at 65 m lying *c.* 10 miles SSW off Rame Head, have a rich fauna which has been studied in detail by Smith (1932). *Montacuta phascolionis* D. & F. a small southern bivalve which is commensal with the sipunculan *Phascolion strombi* (Montagu) was found for the first time in British waters in 1977, four miles east of Eddystone (Gibbs 1978). The coast from Rame Head to Fowey is almost fully exposed to south winds, but again a diversified fauna and flora occurs in the sheltered Fowey estuary (Turk 1971b). St Austell Bay is well-screened from the west and south-west, and deposits in this Bay and Mevagissey Bay are still dominated by china clay waste, although this residue has not been brought to the sea in the formerly characteristic 'white' rivers since the early 1970s. 'Lithothamnium' gravels, the unattached calcareous seaweed known as rhodoliths or maërl and composed mainly if not entirely of the species *Phymatolithon calcareum*, occur in small patches that are mainly dead: it may be that maërl beds have been destroyed by such waste sediments. Within the shelter of Carrick Roads in the Fal Estuary, there are *living* beds of *Phymatolithon* in addition to the extensive subfossil deposits that occur in the Roads and in Fal Bay, and these dead deposits are at present being dredged commercially. Such beds, especially with a representation of living rhodoliths, are localised in Europe, and as these are the only deposits of any significant size in southern Britain, they are particularly important, as a wealth of deposit and suspension feeders, many of them molluscs, are associated with the maërl. Elsewhere in the Bay and the Roads, there is silt and some *Zostera marina*, the eel-grass that is invariably associated with a very diversified fauna. Falmouth Bay and the adjacent coast east of the Lizard are sheltered from westerly winds, and the Bay and its beaches were described, with good reason, as one of the best areas in Britain for the marine biologists in the early years of this century (Clark 1907). A series of papers by W. P. Cocks with long lists and descriptions of molluscs from the Falmouth area, appeared in the *Report of the Royal Polytechnic Society* from 1849 to 1878: Cocks was a regular correspondent of Joshua Alder who visited him and described several of the species that he discovered. Off the Lizard peninsula, the Manacles have become famous diving grounds in recent years, and several rare nudibranchs including *Atagema gibba* Pruvot-Fol have been found. A particularly fine mid-tide and low-water exposure of serpentine occurs at Caerverracks Reef, Kennack, with beautiful weed-filled rock pools and a good fauna of molluscs. At Lizard Point, the Vellan Drang rocks extend some 500 m from high water mark, giving geographers pause for thought regarding the most southerly spot in the British Isles. Mount's Bay on the west side of the Lizard peninsula, is fully exposed to the prevailing winds from the south-west and is largely rocky, but there are more varied deposits in Penzance Bay, another classical collecting ground. Observations made during a holiday, formed the basis of *A naturalist's holiday by the sea* (Sowerby 1923), and the results of many visits to Marazion and St Michael's Mount are summed up in Turk (1974) and SMBA/MBA UK (1978). Shingle bars, in which there is continuous rolling of the particles, have been described as 'intertidal deserts': one such bar cuts off Loe Pool in Mount's Bay and the Swanpool in Falmouth Bay, and except in the more sheltered places such as Marazion where there is a considerable infauna, much of the coarse beach sand of the south coast is mobile and varies considerably, seasonally, in depth. From Mount's Bay to Gwennap Head, there are exposed south-facing granite shores, typically small coves with the substrate covered with granite boulders, as at Porthguarnon and Penberth, but at Porthcurno there is a famous shell-sand beach which acts as a catchment area where millions of small, fresh, unbroken shells can frequently be



collected. It seems certain that many 'Land's End' records that percolated through to J. G. Jeffreys' *British Conchology* would have been based on shells rather than the living animals.

#### THE WEST COAST: LAND'S END TO CAPE CORNWALL

Facing due west, with no land to protect it from any swing of the wind north or south of west, is the blunt nose of Cornwall, presenting six miles of granite cliffs to the Atlantic Ocean. For most of this extent, the granite is largely castellated with few rock pools, and only the hardiest of rocky shore molluscs can survive between tide-marks. Some shelter is evident at Sennen Cove, at the south end of Whitesand Bay. Here there are reefs and good pools, but the mollusc fauna is sparse. The site is described in SMBA/MBA UK (1978).

#### THE NORTH COAST: FROM CAPE CORNWALL TO MARSLAND MOUTH

From Cape Cornwall to St Ives there are high cliffs of granite or greenstone exposed to northerly and westerly winds: here cliff-climbing techniques are practiced by mountaineers. Coves are small and stony but the few rocky platforms as at Tremadda and Treveal near Zennor, have plentiful clean rock pools with numerous species of seaweeds, although algal cover of the platforms themselves is minimal. St Ives to Marsland Mouth on the Devon border, is characterised by high cliffs of Devonian origin as far as Boscastle, and of Carboniferous age from Boscastle to Devon and beyond: the highest cliff in Cornwall is High Cliff, north of Boscastle, which reaches 210 m. The whole stretch of coast is very exposed to northerly and westerly winds and consequent oceanic swell, and the long sandy beaches with high dunes on west-facing bays, act as catchment areas for oceanic flotsam and jetsam as well as local shells which, finely fragmented, form so high a proportion of the blown sand. The sand has been 'on the move' since the 1930s, with sand-blow problems experienced on all the duneland of the north coast, especially in the Hayle, Gannel and Camel estuaries where the sand blows far inland. This is evidently a cyclic problem attributable to shifts in wind direction and strength. Seasonal movements of the beach sand are also a feature, with a tendency for the sand to build up in summer—in time for the visitors—and on occasion to be completely removed in winter. The sand is in general too unstable to contain any permanent infauna, so littoral burrowing molluscs are very scarce on the north coast, being confined to the estuaries. Mud and sand flats with some development of salt marsh are present in the upper reaches of the Hayle, Gannel and Camel estuaries, but possibly because of the shell-sand incursions, the mollusc fauna is not typical i.e. *Macoma balthica* (L.) is absent, *Scrobicularia plana* (da Costa) and *Hydrobia ulvae* are sparse whilst *Phytia myosotis* (Draparnaud) has been recorded only in the Gannel. The cockle *Cerastoderma edule* L. is present in small numbers in Hayle Estuary and the trough shell *Spisula solida* (L.) occurs in the shelter of Daymer near the mouth of the Camel. Immediately off-shore on the north coast, the water is shallower and cooler than off the south coast, but little is known of the fauna except within the shelter of St Ives Bay where extensive recording was undertaken in the early years of this century by Vallentin (1907). Here, at least at that time, there was a reasonably rich fauna of molluscs, and one suspects that many of the 19th century records from 'Hayle' were freshly cast-up specimens from this community. Despite the fresh appearance of a few of the bivalve species, they are probably of very great age, and perhaps even subfossil: valves of *Mactra glauca* Born, *Parvicardium papillosum* (Poli), *Bornia sebetia* (O. G. Costa) and *Divaricella divaricata* (L.) have all been picked up on Hayle sands at various times from 1801 onwards, yet *Divaricella* is the only species to have been found alive north of the Channel Isles when it was dug up between tide-marks on the Isles of Scilly (Fowler 1949, 1950, 1952). It has been



## TURK: CORNISH MARINE CONCHOLOGY

suggested that they might be washed in from subfossil deposits in the Bay, and indeed Vallentin (op. cit.) in a sketch map shows a deposit of blue clay that could conceivably be related to the nearby blue clay of the St Erth Pliocene Beds where many southern species occur (Mitchell 1975). Broad reefs exist at Godrevy, Booby's Bay, Treyarnon to Constantine and again on the stretch of coast from Bude to Marshland Mouth. The pulmonate sea-slug *Onchidella celtica* (Forbes & Hanley) is described as having its headquarters from Newquay to Bude (Gardiner 1939) and certainly it is commoner on the north than the south coast of Cornwall. *Onchidella* is usually associated with mussels, which dominate many of the reefs.

## THE ISLES OF SCILLY

Lying about 27 miles WSW of Land's End, these are the most south-westerly shores of Great Britain and the climate is considerably milder than that of the mainland. The coastline of the five inhabited islands, together with the larger of those that are uninhabited and the numerous islets and rocks, represent only a fraction of the coastline that must have existed before the post-glacial inundation left only small peaks of land above water. It is believed that there was a fall in the sea-level of *c.* 90 m (Mitchell 1960) and that they were cut off from the Cornish mainland as recently as 8000 B.C. The drowning of the land has resulted in sites as interesting as they are beautiful, with a range of habitats and shelter not immediately recognized by naturalists in the mid-19th century. It was the 1880s when Smart and Cooke (1885 & 1886) drew attention to the wealth of molluscan life, much of it associated with *Zostera marina*, then growing luxuriantly, and covering hundreds of acres of flats, encircled and sheltered by the larger islands. The decline of *Zostera* in the 1930s here as in all its sites on the mainland, with the attendant dispersal of the organic silts, is fully discussed by Wilson (1949). Its reduction in coverage and size has adversely affected the animal communities, but there are still large numbers of molluscs, particularly bivalves, in and on the sand flats, and *Zostera* continues to grow locally between the islands. The flats are of coarse granitic sand, similar to off-shore shell-gravels elsewhere and in shelter approaching that of an estuary. The work of London University Sub-Aqua Club in 1959 and the early 1960s has greatly extended the knowledge of sublittoral sites, and the findings are summarised by Harvey (1969a). In general, physical conditions are a continuation of what occurs between tide-marks except that boulder slopes, which extend steeply some 30 m below sea level, are characterised by even larger boulders than there are on the more exposed shores. In places, the castellated granite, as at Pendennis Head, is continued below water, with deep gullies where there are faults in the rock. Huge oarweeds dominate the surfaces to the 30 m level, below which the walls and gullies are 'richly encrusted' with animal life, and horizontal surfaces carry 'an heterogenous carpet' of sponges, tunicates, hydroids and sparse red algae over which creep 'large numbers of rissoids, polychaetes and amphipods'. The sand of the Scillies is very white, revealing the preponderance of felspar and it is mobile in exposed positions where it forms small dunes.

## NOTES ON THE GROUPS AND SELECTED SPECIES

A total of nearly 500 species of molluscs has been recorded from the shores and shallow water of south Cornwall alone (Sea Area 18 in part). Numbers are smaller for the Isles of Scilly (Sea Area 19) and much smaller for north Cornwall (Sea Area 20 in part), and with few exceptions all species found in Scilly and north Cornwall are also present on the south Cornish coast. Significantly North Cornwall has less than half as many species recorded live as are known from the south coast, whereas the number known only from shells is twice as many. No less



than 60 species are known only from shells in the three Sea Areas under consideration and a quarter of these are based on 19th century records. Little is known about the transport of shells, their break-up rate in various conditions, allowing for differing thickness, or their dissolution in the acid conditions of mud flats (Holme 1965), so care must be taken in the interpretation of such records. Holme (op. cit.) has found that sediment in the English Channel is 0.20–0.30 m deep on average, and that ‘perhaps 10 cm’ of this deposit represents shells still to be found in the vicinity: reckoning on about 0.01 m accretion per 1000 years, he believes that such a deposit could be thousands of years old. He found evidence that there was ‘little or no transport along the sea bed’ in the depths of 8 to 95 m in which he dredged at 300 stations, whilst accepting that in shallower water, both living and dead shells are carried by tides to be cast ashore. The presence of land snails in a bank of shells lying *c.* 18 m in St Ives Bay, together with a number of shore species, indicates movements at a considerable depth away from the shore as well as towards it. Unfortunately, the data is often minimal in the many lists and collections of the last century, and there is rarely an indication of whether the animals were found alive *in situ*, alive but cast up or as shells only: when the venue is a place noted for its shell sand, such as Porthcurno, Harlyn or Hayle, one suspects that finds were based on shells alone.

#### HISTORICAL RESUMÉ OF MARINE CONCHOLOGICAL STUDIES IN CORNWALL AND THE ISLES OF SCILLY

The earliest chroniclers of the natural history of Cornwall and the Isles of Scilly, either ignored the conchological aspect, or spoke in generalities about the oysters, cockles, mussels and ‘wrinkles’. It was not until 1758 that William Borlase (1696–1772), a Cornish clergyman, wrote more specifically, describing and figuring a number of marine molluscs in his *Natural History of Cornwall*. He corresponded with many naturalists, but a few decades passed before such conchological visitors as J. T. Swainson (*c.* 1750–1825), George Montagu (1751–1815), William Turton (1762–1835) W. E. Leach (1790–1836) and Joshua Alder (1792–1867) were to visit Cornwall. In 1841 another Cornishman, Jonathan Couch, a surgeon, published ‘The testaceous mollusks’ as part of his *Cornish Fauna*. The following year, 1842, William Pennington Cocks (1791–1878), also a surgeon, retired to Cornwall and commenced his study of the Falmouth fauna which occupied him until his death, and which had its main fruition in 1849 with a long paper in the *Report of the Royal Cornwall Polytechnic Society*, whilst his artistic gifts are enshrined in two MS books owned by the Polytechnic Society, of paintings and sketches of the Falmouth fauna, containing many illustrations of rare molluscs. Both these men, like Borlase before them, carried on a very considerable correspondence with other naturalists throughout Britain. The broader interconnections of local and national studies in Cornish natural history from 1700–1900 are reviewed in detail by F. A. Turk (1959).

The 19th century included 24 people who were to become involved in varying degrees in Cornish conchology, ten of them as visitors to the county: amongst these were Edward Forbes (1815–1854), J. G. Jeffreys (1808–1885), R. MacAndrew (1803–1873) and Clifford Burkhill who died, still a young man, in 1891, and who collaborated with J. T. Marshall in studying Scillonian shells (Burkhill and Marshall 1889, 1891). They, together with Jeffreys and Sylvanus Hanley (1819–1899) were among the early members of the Conchological Society, founded in 1876. Hanley spent the last year or so of his life at Penzance where he received honorary membership of the Penzance Natural History and Antiquarian Society. In 1866, Williams Hockin (1804–1874), a Cornish solicitor, published, anonymously, a list of Cornish marine shells, based on his own finds as well as the collection made by his father-in-law, James Tilly, captain of one of the famous Falmouth Packets. The records of 15 other Cornish



men and women were included in Cocks's notes in the *Reports* of the Royal Cornwall Polytechnic Society and the lists of Tregelles (1885, 1896): George Fox Tregelles lived from 1859–1943, was a member of the Conchological Society, and published his second paper in its *Journal*. These 15 collector/recorders included Miss Elizabeth Carne (1817–1873), Miss Hannah Tyacke (c. 1820–c. 1900), Miss Elizabeth Vigurs (c. 1810–1890) and her brother, a surgeon, Richard C. Vigurs (1820–c. 1900).

Conchologists whose lives span the 19th and 20th centuries, number over 60 of whom nearly 40 were visitors to the Duchy, and of whom 28 were members of the Conchological Society, reflecting its rising influence. With 15 professional biologists, (one of them, Marie Lebour, a woman), compared with only two professionals in the 19th C., one finds the first influence of the Marine Biological Association of the United Kingdom, founded at Plymouth in 1884, with names like E. J. Allen (1866–1942), L. R. Crawshay (1868–1943), J. T. Cunningham (1859–1935) and Walter Garstang (1868–1949) in the conchological literature. Several other scientists—then always known as ‘naturalists’—a few of them in an honorary position, contributed molluscan records which appear in the editions of the *Plymouth Marine Fauna* (M.B.A. 1904, 1931, 1957). Two of the men who settled in Cornwall, Rupert Vallentin (1859–1934), an amateur of the highest professional standards who lived in the county from 1887–1925 (apart from visits to the Falklands) and James Clark (1861–1935), Principal of Truro Technical Schools from 1899 until 1907, contributed an immense amount to the knowledge of the Cornish molluscan fauna. The former published a series of papers concerned primarily with plankton and nudibranchs in the *Journal* of the Royal Institution of Cornwall, and the latter brought together records of all known Cornish species of marine Mollusca in the *Victoria County History*, published in 1906: both men worked in close collaboration with members of the staff at the Marine Biological Association's Laboratory. R. W. J. Smart (c. 1850–1905) was curator-in-charge of Tresco, Isles of Scilly from 1879–1884, and in collaboration with A. H. Cooke (1854–1934), another clergyman and author of ‘Molluscs’ in the Cambridge Natural History Series, published a list of all known records from the Isles of Scilly (Smart and Cooke 1885, 1886). The unpublished records of many conchologists at the turn of the century, were garnered in the second paper by Tregelles (1896) and Clark (1906). J. T. Marshall (1892–1922) cites other recorders as well as the results of his personal collecting in Cornwall, in his long series of papers in the *Journal of Conchology* from 1893–1917, adding to the information in J. G. Jeffreys' *British Conchology*. It is significant that Garstang, Smart, Cooke, Clark and Marshall were all members of the Conchological Society. From 1924 when the Society's Marine Census was started by Ronald Winckworth (1884–1950), records have been brought together by the marine recorders, every one of which has done some personal recording in Cornwall, including Winckworth himself when he worked for a short time at the M.B.A. Laboratory: successively, the recorders have been A. P. Gardiner (Recorder 1932–52, and resident in Cornwall from 1906–c. 1911 and subsequent visits; Mrs Nora F. McMillan (Recorder 1952–61, with a recording trip to the county and the Isles of Scilly in 1980); David Heppell (Recorder 1962–66, recorded in Cornwall, 1962 and 1981); S.M.T. (Recorder 1966–72, and resident since 1931); Dr. Shelagh M. Smith (Recorder 1974–75, recorded 1981); C. P. Palmer (Recorder 1975–78 and recorded in Isles of Scilly 1972–1981); and D. R. Seaward (Recorder since 1978, recorded in Cornwall 1978 and Isles of Scilly in 1982). Noted for his indefatigable collecting and his search for the biggest and most perfect specimens, was Conchological Society member T. G. W. Fowler (1880–1967) who lived in Cornwall for the last years of his life, but travelled widely on collecting trips. Taking a taxi to the most productive soft substrate shores at the lowest tides, and digging in an unrestrained fashion to collect the largest possible number of specimens, is now considered as irresponsible as netting butterflies in quantity. His resultant collections, necessarily outstanding, are mainly in the British Museum (Natural History), with some in the Isles of Scilly and Merseyside Museums.



A summary of 20th century conchologists, shows a total of about 140 individuals, of whom over 100 have been visitors to Cornwall, compared with about 40 in the 19/20th C. span, whilst professionals also number 100, approximately four times as many. Since 1974, the number of scientists undertaking research on the Cornish side of the Tamar from the Marine Biological Association Laboratory (where now in 1982 there is staff of 100 full-time scientists and, annually, over 180 visiting scientists) and from Ministry of Agriculture, Fisheries and Food laboratories, has been augmented by those from the Institute of Marine Environmental Research. Concern about growing environmental pressures on shores and shallow seas, has alerted the Nature Conservancy Council to the necessity of evaluating marine sites, and consequently the Council has sponsored the investigation of parts of the coast (Intertidal Survey Unit) and shallow seas (South West Britain Sublittoral survey): both groups have published reports on parts of the Cornish coast. In 1975, the South West Marine Biology Study Group was formed, and although in abeyance since 1979, under the joint Chairmanship of Dr. Norman Holme and Professor David Nichols, much material was brought together and the specially-designed field cards for both rocky and sandy shores are the basis for marine recording of the University of Exeter's Cornish Biological Records Unit: molluscs are amongst the indicator species. Various universities, including Bristol, have initiated records through post-graduate research students and groups of students on educational courses. Exeter University, through its Zoology Dept, Extra-Mural Dept and Institute of Cornish Studies (established 1971), with the associated Cornish Biological Records Unit, has played a noteworthy part in mollusc recording. Field days organised by the Lizard Field Studies Club (founded 1953), Camborne-Redruth Natural History Society (1956) and Cornwall Naturalists' Trust (1962) have also been a source of records.

These days, inter-relationships are more complex, group undertakings are more frequent, more and more papers are written by several authors, often involving a multi-disciplinary approach to only one species or a single function or structure of a species; but with it all, the amateur in the more professionalised attitude made possible by modern education, still plays an important part: the Conchological Society has done much to enhance the reputation of the amateur through its Junior Membership, *Papers for Students* publications and the Marine Census Scheme.

#### THREATS TO MARINE LIFE

The effects of the holiday trade in the South-West are well summarised by Harvey (1969b) in the following words 'Tourism, although a mild price to pay for freedom from urbanisation, nevertheless carries its penalties in the thoughtless erosion of natural areas by holiday makers, a phenomenon which is particularly apparent on some shores where the constant turning and treading of boulders and pools has seriously diminished the fauna and flora. Furthermore, the provision of accommodation, whether by boarding-house or caravan-park, and the development of facilities such as promenades and the like to tidy up a shore are inexorably encroaching more and more on the natural ecological features of coast and countryside.' Such pressures are unlikely to lessen, and indeed with improved roads combined with more reliable weather forecasts, one can be sure that fine weather will concentrate even more people on the beaches: as it is, the human population at least doubles, in the various resorts during the summer, and pollution by increased sewage outfall can be measured by the decrease in diatom diversity (Hendey 1977). Fortunately for marine life, the most popular beaches are on the north coast (Calder 1976) where the fauna and flora are less diversified on the reefs, and the sand is largely barren, although the trampling of fore-shore dunes presages disaster for many dune species.

With angling still increasing as a popular sport, greater disturbance is resulting from the



search for soft crabs on rocky and stony shores, and worms and razor-fish on those with soft substrate. Few such collectors replace stones or back-fill holes that they dig, and in any event some irremediable damage will have been done by digging in the first instance.

Littoral food-collecting is another pressure. Cockles are collected in very large numbers from comparatively small areas: traditionally this is on Good Friday when as many as a thousand or so people congregate at certain points in Helford Estuary and Gillan Inlet, but cockles are gathered at many other times of year as well. Mussels and to a lesser extent limpets are also taken, and in the past decade or so, periwinkles have been added to the list: these are not often for home consumption as is usual elsewhere in the country, but for export to meet a seemingly insatiable demand in France and Spain. The current price to shore collectors in Cornwall in February 1982, was £12 a cwt, and the trochid *Monodonta lineata* was being collected with *Littorina littorea*.

The effects of educational groups—schools, colleges and universities—can be considerable especially when digging in soft substrate is involved. Moreover, concentration of visits on easily-accessible sites is the general pattern. As has been discussed, many species which elsewhere in British coastal waters, live only off shore, in Cornwall may also be found between tide-marks, and as a number of these are unusual and long-lived southern forms, the communities that they form are unique and worth protection. The very fact that they are littoral, puts them at greater risk.

As other parts of Britain, such as the Severn and part of N.E. Britain, become more polluted, so increasing numbers of divers, like the educational shore parties, choose the far S.W. for their holidays. Many individual divers are members of the Underwater Conservation Society and/or the British Sub-Aqua Club Association which both have strict rules of conduct, but there are still many souvenir hunters collecting the sea-urchin *Echinus esculentus* and the coral *Eunicella verrucosa*. The former, which sometimes carries the rare external molluscan parasite, *Pelseneeria stylifera* (Turton), is now exceedingly rare at low water in those few places where formerly it was common, whilst the latter grows very slowly and is often host to the scarce southern prosobranch *Simnea patula* (Pennant) as well as certain species of nudibranchs. The commercial dredging of the calcareous seaweed *Phymatolithon calcareum* in the Fal must be destructive of vast numbers of organisms, including molluscs.

Industrial effluents occur even in Cornwall, and indeed Devoran Creek in the Fal Estuary has the distinction of being one of the water-ways in Britain most polluted with heavy metals (Holliday and Bell 1981). Until the early 1970s, china clay residue was discharged into St Austell and Mevagissey Bays, and there is a legacy of soft clay deposits. At the present time, large amounts of 'tailings' from South Crofty tin workings, near Camborne, flow into St Ives Bay at Gwithian via the well-named Red River Valley. Last but not least, as was shown by 'Torrey Canyon' of bad memory, Cornwall is particularly vulnerable to spillages from oil-tankers passing up the Channel.

The need for monitoring the shores and shallow seas in Cornwall, and the desirability of establishing Marine Nature Reserves and voluntary Marine Nature Conservation Areas becomes increasingly obvious. Cornwall welcomes visits from all those—amateur and professional, learners and learned alike—who wish to study the fauna and flora; long may the tradition of Cornwall attracting such attention continue; but we must all step gently just because there are more of us to tread on marine and maritime areas already reduced in size and diversity.

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# THE CONCHOLOGICAL COLLECTIONS OF BRUGUIÈRE AND OLIVIER FROM THE OTTOMAN EMPIRE (1792–1798)

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*Abstract:* A brief account is given of the lives of Bruguière and Olivier, and of their travels in the Ottoman Empire. Types of the land and freshwater mollusc species described from material collected on the expedition, excluding those described by Férussac, are listed and figured.

## INTRODUCTION

In 1792, the then French Ministre de l'Intérieur, Jean-Marie Roland, took the decision to send a scientific expedition to the Middle East. Bruguière and Olivier were selected to carry out the mission and spent a total of six years travelling. Bruguière died on the return journey, but Olivier was able to bring back many important collections including nearly one hundred species of land and freshwater Mollusca. These collections were deposited in the Muséum National d'Histoire Naturelle, Paris (MNHN), where they have remained since that time.

Basic biographic information on Bruguière and Olivier has been taken from Theodorides (1962), Lamy (1930), and Silvestre (1815); additional information is taken from various archives cited in the text.

## THE LIFE OF BRUGUIÈRE

Jean-Guillaume Bruguière was born in 1749 in Montpellier. The son of a surgeon, he was awarded his Doctorate of Medicine at Montpellier in 1770. He never practiced, but went to Paris to study botany. In 1773 he took part, as a zoologist, in Kerguelen's second expedition to the austral lands, and collected molluscs and vertebrates in Madagascar. The expedition failed to colonise the Kerguelen Islands (which Kerguelen himself had referred to as 'la France australe') and Kerguelen was condemned to jail. As a result no natural history reports of this expedition were ever published. The shells were acquired from Bruguière's widow by the MNHN in 1799 (Archives nationales F17/3905), but were relabelled in such a way that it is practically impossible to recognise them in the collections.

By 1774 Bruguière was back in Montpellier where, in 1776, he was elected an associate member of the Botanical Section of the Société des Sciences et Belles-Lettres. He tried to develop coal mining in the area and at the same time became interested in fossils; it was probably during this period that he got to know Olivier and Broussonet. Pierre Marie Auguste Broussonet had been awarded his Doctorate of Medicine in 1779 in Montpellier at the age of 18, as a result of which it was proposed that he succeed his father as Professor at the University. However, his nomination was refused because of his age, and he went to England where he worked with Banks on the Cook fishes. There he met the Intendant de Paris,

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Berthier de Sauvigny, and it was with his help that, on his return to Paris, Broussonet was appointed secretary of the Société d'Agriculture. Here Broussonet regularly met with a number of Parisian naturalists, among them Daubenton whom he introduced to Bruguière. When Daubenton was later asked to describe the Vermes in the *Encyclopédie Méthodique* he entrusted the task to Bruguière. Bruguière had arrived in Paris in 1781 and all that is known of the next few years is that he tried to travel to the West Indies and South America: on the 8th March, 1784, he wrote a letter from Montpellier asking for funds (Archives de l'Institut). In 1787 he was nominated for the post of Botanist in Saint-Domingue, but Louis Claude Marie Richard, who was Botanist in Cayenne, obtained the position and Bruguière was indemnified (Archives nationales, Ministère des Colonies, E54). Although a Republican, he lost most of his income at the onset of the French Revolution (letter, 26.6.1791, Archives de l'Institut). In 1792 Bruguière collaborated with his friends Lamarck and Olivier in starting the *Journal d'Histoire Naturelle*, but he was probably near the end of his financial resources when Olivier proposed their journey to the Middle East.

#### THE LIFE OF OLIVIER

Guillaume-Antoine Olivier was born near Toulon in 1756. The son of a physician, he studied medicine with Broussonet in Montpellier, obtaining his Doctorate in 1776. He had been interested in botany and entomology from this time and wished to join Broussonet in Paris, but his father refused him the necessary funds and he was forced to practice as a physician near Montpellier. In 1783, Berthier de Sauvigny wished to obtain various statistics on his intendency. Broussonet recommended Olivier for the job, enabling him at last to join Broussonet in Paris. In 1789, on the very day of the taking of the Bastille, Berthier de Sauvigny was assassinated and his house sacked; only a part of Olivier's manuscript was saved.

Gigot d'Orcy, Receveur General des Finances and an amateur entomologist, wished to publish an account of the natural history of insects. He employed Olivier who travelled to England and Holland, and it was probably during this period that he met Thomas Martyn in London (letter of recommendation, undated, Muséum MS 1998 (II), Fol. 235). In 1789 and 1790 he published the first two volumes of the *Histoire naturelle des Coléoptères* for Gigot d'Orcy, and simultaneously, thanks to Daubenton's recommendation, collaborated in the *Dictionnaire de l'Histoire naturelle des Insectes, Papillons, Crustacés, etc...* Olivier lost his position when Gigot d'Orcy was guillotined. In 1792 he collaborated in the *Journal d'Histoire Naturelle*. During this time Broussonet had been appointed a deputy at the Etats Généraux, and later at the Convention, where he had joined the Girondist party. This party was at the height of its power at the end of 1792, and it was probably easy for Broussonet to obtain from Roland, also a Girondist, permission to send his friends Bruguière and Olivier to the Middle East.

Olivier returned from the voyage alone, but with the collections, in 1798. As early as January, 1799, he was elected an associate member of the Institut de France, and replaced Daubenton as a full member in the Section of Anatomy and Zoology in March, 1800. The account of the journey to the Middle East was published between 1802 and 1807, either as three 40 volumes or six 80 volumes, plus an atlas, under the title: *Voyage dans l'Empire Ottoman, l'Egypte et la Perse, fait par ordre du Gouvernement, durant les six premières années de la République*. He was appointed to the examining board of the Veterinary School of Alfort in 1809, and Professor of Zoology there in 1811. However, he was by then a sick man and died from a heart attack in Lyon in 1814 at the age of fifty-eight.



## THE VOYAGE IN THE OTTOMAN EMPIRE

Bruguière and Olivier left Paris in November, 1792. Their mission was originally to collect natural history objects, but was later to become diplomatic; France was under attack from the rest of Europe, and the French government decided to re-establish relations with Persia, which at that time was at war with Russia. They set sail for Istanbul on the 22nd April, 1793, arriving one month later. During the journey the French ambassador had been recalled, and his replacement had to wait nine months for his instructions from Paris. As a result, Bruguière and Olivier decided to visit the eastern Mediterranean; they travelled along the Turkish coast and visited the Greek archipelago and Egypt, returning to Istanbul in April, 1795. Despite the blockade against French ships, they were able to send seeds back to the Muséum during this period (letter sent to Thouin from Alexandria, 3rd Prairial An III, Archives de l'Institut). In Istanbul they met the new ambassador who was able to give them instructions for the Persian government. They travelled to the Syrian coast, and in Aleppo joined a caravan to Baghdad, arriving there on the 25th April, 1796. The continuation of their journey was greatly facilitated by Olivier's ability to cure a certain Pacha Suleyman of an illness in only three days, when he had been considered at the point of death by his own physicians; the vice Pacha, who had assumed his master's title during his illness, was executed!

Bruguière and Olivier left Baghdad on the 18th May, 1796, with a caravan bound for Kermanshah where they joined a Persain officer who was to act as their guide to Tehran. They visited the rock inscription of Darius at Bisotun and climbed Mount Alvand. During the last stage of the journey to Tehran, where they arrived on the 2nd July, Bruguière was taken seriously ill. At this time the king, Aga Mohammed Khan, was away attempting to conquer Khorasan. Bruguière and Olivier at first wanted to join him there, but finally waited, and when he returned on the 20th September he granted them an interview with the Prime Minister.

At this point they decided to start their return journey. They visited Qom and Esfahan, and arrived back in Kermanshah on the 1st December. Between Kermanshah and Baghdad Olivier was wounded by Kurdish bandits. Although they wished to return to Europe as quickly as possible, they were detained in Baghdad until May, 1797, by the chief janissary whom they were curing of venereal disease. They finally left Baghdad, travelling to Latakia via Aleppo; the journey lasted from May to the beginning of September. They were able to sail to Cyprus and then Gilindire on the south coast of Turkey, and travelled through Turkey to Istanbul. Here they rested for five months while they gathered together their collections. Further travel was delayed as a result of the English policy against France, and they were only able to sail from Istanbul in May, 1798. On the journey they visited Athens and Corfu, and arrived at Ancona in Italy on the 19th September. Bruguière, who had apparently felt rather better since their stay in Istanbul, developed a strong fever and died on the 3rd October, 1798. Olivier returned alone with the collections, finally reaching Paris in December, 1798.

## THE MOLLUSC COLLECTIONS

Hamy (1908) states that Olivier deposited the collections in the MNHN on the 14th prairial, an VIII, i.e. 3rd June, 1800. On the 25th September the same year, the aide-naturaliste Desjardins produced a report describing the poor state of preservation of the collection, which he considered to be at risk. In 1819 the then aide-naturaliste Valenciennes established an inventory of the Olivier shells housed in the MNHN (Archives nationales AJ15/550). This



lists 74 non-marine species (including 57 land snail species), many of them indicated as new, and including most of the types described by Olivier. In November, 1820 Férussac produced a manuscript catalogue of the land shells preserved in the MNHN (Laboratoire de Malacologie, MNHN). This catalogue forms the first manuscript of the *Prodrome* published in 1821. It mentions only 22 species as having been collected by Olivier, whereas in the text of the *Prodrome* 47 species of land snail are named as communicated by Olivier. At present the MNHN collections include two sets of samples labelled as collected by Olivier: one is labelled 'M. Olivier, 1819' and fits Férussac's inventory of 1820; the second was acquired as part of the Férussac Collection in 1837, and is in agreement with the *Prodrome*. It can thus be deduced that most of Olivier's land shells were acquired by Férussac from the MNHN between March, 1819, and November, 1820. They may have been given, exchanged, sold or even bequeathed to Férussac by Olivier; this last possibility is suggested by Bourguignat (1853) who unfortunately does not cite his sources, and who was sometimes unreliable. Whatever happened, it is clear that the collection of shells brought back from the 'Voyage dans l'Empire Ottoman' has remained housed in the MNHN since 1837.

#### TAXA DESCRIBED FROM OLIVIER'S MATERIAL

Six authors utilised the molluscan collections made by Olivier and Bruguière for the description of new taxa:

1. Olivier himself described and figured 22 species in the first and second livraisons of the account of their travels, published in 1801 and 1804. According to Bourguignat (1853), Olivier simply transcribed Bruguière's notes; although this is quite probable, it is based solely on Bourguignat's personal opinion.
2. Cuvier described *Parmacella* as a new genus (type species *Parmacella olivieri*) in 1804 from specimens collected by Olivier in Mesopotamia.
3. In 1821, Férussac introduced 23 new names based on Olivier's material; these were progressively validated either by Férussac himself or by other authors. These names and their types will not be treated here, but in a separate paper.
4. Bourguignat (1853) described five new species of *Unio* from Olivier's material; two were given by Bourguignat as Férussac manuscript names. This is confirmed by the labels, but the authority of all five must be attributed to Bourguignat.
5. Lamarck, as professor, and responsible for the collections of molluscs from 1793 to 1829, used Olivier's material for his work. Only one new Lamarckian name based on these shells has been traced, i.e. *Cyrena cor*.
6. Cailliaud described several new species of Egyptian molluscs between 1823 and 1827, but apparently based only one, *Cyrena consobrina*, on Olivier's material. Cailliaud, most of whose types are housed in the MNHN, associated with Férussac, de Blainville, and Deshayes. Indeed, the labels of his types suggest that the species which he described were named by Férussac (it may be noted that he never wrote 'I name this species...', but rather 'This species was named...'). It is therefore highly probable that his descriptions were based on Olivier's material as well as his own, but he mentions this only in the case of *Cyrena consobrina*.

#### LIST OF TYPES

Taxa are listed hereafter in alphabetic order of specific name. Many lots are listed as 'probable syntypes' as the modern type concept did not exist in the first half of the nineteenth Century. Specimens were often relabelled and the original label destroyed as soon as a synonymy was established. The absence of any type concept is also the reason why so many



types are missing from the older museums; curators did not hesitate to give away or exchange the type specimens when they had obtained a better-preserved specimen thought to belong to the same species. Most of the Bourguignat types are listed here as 'probable holotype' as he never mentions the number of specimens in his possession and it is no more than probable that there was a single type specimen in each case. No lectotypes are selected here as we consider this to be the responsibility of a revisor, not a curator. Where appropriate, comments on the current taxonomic status and geographical distribution of the species have been included.

*bagdadensis* Bourguignat 1852, *Unio*. pl. 7, fig. 2

Bourguignat 1852, p. 30, 1853, p. 78, pl. 4, figs. 4–6. Type locality: R. Tigris, Baghdad. Probable holotype, figured by Bourguignat, Baghdad. Distribution: Iraq.

*bruguierianus* Bourguignat 1853, *Unio*. pl. 7, fig. 5

Bourguignat 1853, p. 78, pl. 2, figs. 54–56. *Nomen novum* for *Unio orientalis* Bourguignat 1852, *nec* Lea 1840. Listed by Haas (1952, p. 119) as a subspecies of *Unio crassus* Philipsson 1788.

*buccinoidea* Olivier 1801, *Melania*. pl. 5, fig. 11

Olivier, 1801, I, p. 297, pl. 17, fig. 8. Type localities: Greek Archipelago, Crete, Syria. Ten possible syntypes, labelled '*M. praemorsa* L., Tripoli, M. Olivier, 1803'. The original description of *buccinoidea* mentions only the coasts of Syria, not specifically Tripoli. Tripoli is mentioned by Férussac (1822, p. 21) but it is uncertain whether he obtained this sample from Olivier. Synonymised with *Melanopsis praemorsa* (L. 1758) by Germain (1921, p. 477). Distribution: Circum-mediterranean.

*bulimoides* Olivier 1804, *Cyclostoma*. pl. 5, fig. 7

Olivier, 1804, II, p. 39, pl. 31, fig. 6. Type locality: Kalidje, Egypt, 'inside a mummy of an Ibis'. Three probable syntypes. These specimens were named '*Cyclostoma impressum* Draparnaud' by Valenciennes in his inventory of 1819, and were relabelled '*Bithynia impura* Draparnaud'. Fortunately their locality is so unusual that there is no doubt about their status. Type-species of *Cleopatra* Troschel 1856. Distribution: Central and North-east Africa.

*carinata* Olivier 1804, *Cyclostoma*. pl. 5, fig. 3

Olivier 1804, II, p. 39, pl. 31, fig. 2, A, B. Type locality: Canals in Alexandria, Egypt. Five syntypes, 'Alexandria, in canalis', with a label probably written by Olivier giving a reference to the original figure. Four probable syntypes relabelled '*Ampullaria bolteniana* Fér.' Type-species of *Lanistes* Montfort 1810. Distribution: North and East Africa.

*cariosa* Olivier 1804, *Helix*. pl. 6, fig. 5

Olivier 1804, II, p. 221, pl. 31, fig. 4a, b. Type locality: Beirut. Eight syntypes, Beirut; two shells not mentioned in the original description, Tripoli. The type species of *Sphincterochila* (Rima) Pallary 1910. Distribution: Middle East.

*castanea* Olivier 1801, *Helix*. pl. 6, fig. 1

Olivier 1801, I, p. 224, pl. 17, fig. 1a, b. Type locality: Istanbul, Gemlik. Three probable syntypes, Constantinople. This sample comes from the Férussac collection, and Férussac's label does not indicate whether it came from Olivier, but this is highly probable. Name preoccupied by *Helix castanea* Müller 1774, and consequently changed to *Helix mahometana* by Bourguignat (1860).

*consobrina* Cailliaud 1827, *Cyrena*.

Cailliaud 1827, IV, p. 263; Atlas, II, pl. 61, figs. 10–11. Type locality: Egypt. Based on specimens collected by both Olivier and Cailliaud. Six complete probable syntypes, Egypt, labelled '*Corbicula orientalis* Lk.'; not mentioned in the 1819 inventory. According to



Germain (1922, p. 93) a junior synonym of *Corbicula fluminalis* (Müller 1774). Distribution: Middle East, North-east Africa.

*cor* Lamarck 1818, *Cyrena*

Lamarck 1818, p. 562. 'Mon cabinet; communiquée par Olivier venant de son voyage'. Seven complete probable syntypes, Syria, labelled '*Corbicula fluminalis* Müller var. *cor* Lk.' and '*Corbicula orientalis* Lk.' Original labels lost. Synonymised with *Corbicula fluminalis* (Müller 1774) by Germain (1922, p. 92).

*costata* Olivier 1804, *Melania*.

Olivier 1804, II, p. 294, pl. 31, fig. 3. Type locality: canals in Gesser-Choure (=Jisr esh Shughar, Syria). This species is not mentioned in the 1819 inventory of Valenciennes; the sample collected by Olivier was not found, only a single fossil shell from Sestos, mentioned by Férussac (1822, p. 28). Referred to *Melanopsis* Férussac 1807 by Germain (1921, p. 489). Distribution: Middle East.

*crenulata* Olivier 1804, *Helix*. pl. 6, fig. 4

Olivier 1804, II, p. 40, pl. 31, fig. 5a, b. Type locality: Column of Pompeius, Alexandria (Egypt). Nine syntypes, labelled as coming from Olivier, original labels lost. Three probable syntypes, Férussac Collection; not indicated as having been collected by Olivier, but labelled 'close to the column of Pompeius' which is the published type locality. The name is preoccupied by *Helix crenulata* Müller 1774. Bourguignat (1863, p. 66, pl. 10, figs. 4–6.) described a new species, *Helix ptychodia*, from northern Egypt, stating that *H. crenulata* Olivier was merely a form of *ptychodia*; it was not expressly proposed as a *nomen novum*. *Helix ptychodia* is the type-species of *Trochoidea (Xeroptyca)* Monterosato 1892. Distribution: North-east Africa, ? Syria.

*denticulatus* Olivier 1801, *Bulimus*. pl. 5, fig. 12 and pl. 6, fig. 10

Olivier 1801, I, p. 297, pl. 17, fig. 9a, b. Type locality: Khios, Greece. The sample from Khios was mixed, probably by Férussac, with another attributed to the same species but collected by Olivier in Gemlik (Turkey), and which appears different. A further sample, from Beirut, was also determined as *B. denticulatus*. Type-species of *Laciniaria (Denticularia)* Lindholm 1924. Distribution: Balkans.

*euphraticus* Bourguignat 1852, *Unio*. pl. 7, fig. 1

Bourguignat 1852, p. 28, pl. 4, figs. 1–3. Type locality: Baghdad, Iraq. Probable holotype, figured by Bourguignat, Baghdad. Type-species of *Leguminaia (Pseudodontopsis)* Kobelt 1913. Distribution: Iraq.

*fasciolata* Olivier 1804, *Melanoides*. pl. 5, fig. 2

Olivier 1804, II, p. 40, pl. 31, fig. 7. Type locality: Kalidje, Egypt. Four syntypes, labelled 'an Syria? an Alexandria?' Type-species of *Melanoides* Olivier 1804. Synonymised with *Melanoides tuberculata* (Müller 1774) by Germain (1921, p. 453).

*fasciolatus* Olivier 1801, *Bulimus*. pl. 5, fig. 8

Olivier 1801, I, p. 416, pl. 17, fig. 5. Species based on specimens from Crete, Rhodes, Syria, and 'Caramanie' (=southern Turkey). Three samples: Twelve syntypes, Rhodes; five syntypes, Rhodes and Latakia; twelve syntypes, 'côtes de Caramanie'. Referred to *Zebrina (Zebrina)* Held 1837 by Fuchs and Käufel (1936, p. 573). Distribution: Crete, Rhodes, Cyprus, Middle East.

*guttata* Olivier 1804, *Helix*. pl. 6, fig. 2

Olivier 1804, II, p. 334, pl. 31, figs. 8a, b. Type locality: Urfa, Turkey. Four syntypes, Urfa. Type species of *Levantina (Assyriella)* P. Hesse 1908. Distribution: Middle East, ?Sicily.



*inflatus* Olivier 1801, *Bulimus*. pl. 6, figs. 8 and 9

Olivier 1801, I, p. 417, pl. 17, figs. 3a, b. Type locality: Crete. Eleven syntypes, 'Candie' (=Crete); original label lost. Referred to *Albinaria* Vest 1867 by Nordsieck (1977, p. 303). Distribution: Crete.

*labrosus* Olivier 1804, *Bulimus*.

Olivier 1804, II, p. 222, pl. 31, figs. 10a, b. Type locality: Beirut, Lebanon. Types not listed by Valenciennes in 1819, nor seen by Férussac for the Prodrome (1822, p. 55). Type species of *Buliminus* Beck 1837.

*mahometana* Bourguignat 1860, *Helix*, pl. 6, fig. 1

Bourguignat 1860, p. 172. *Nomen novum* for *Helix castanea* Olivier 1801 nec Müller 1774. Listed by Germain (1921, p. 127) as a variety of *Helix lucorum* L. 1758. Distribution: Middle East, Italy.

*olivieri* Cuvier 1804, *Parmacella*.

Cuvier 1804, p. 435, pl. 19, figs. 12–15. Type locality: Mesopotamia. One syntype, preserved in liquid but not dissected, Mesopotamia. Not found by Férussac (Histoire II, 1, p. 79). Type species of *Parmacella* Cuvier 1804. Distribution: Iran, Iraq.

*orientalis* Olivier 1801, *Planorbis*. pl. 5, fig. 4

Olivier 1801, I, p. 297, pl. 17, figs. 11a, b. Type locality: Khios. Sixteen probable syntypes, Scio (=Khios), Férussac collection. Fuchs and Käufel (1936, p. 543) list this as a subspecies of *Planorbis planorbis* (L. 1758). Distribution: Khios.

*orientalis* Bourguignat 1852, nec Lea 1840, *Unio*. pl. 7, fig. 5 Bourguignat 1852, p. 29.

= *Unio bruguierianus* Bourguignat 1853, p. 78, pl. 2, figs. 54–56. Type locality: R. Simoïs, Turkey. Syntypes: two complete specimens, including the one figured by Bourguignat, plus one valve, Simoïs river. Two valves, Constantinople, not mentioned in the original description.

*ovata* Olivier 1804, *Ampullaria*. pl. 5, fig. 1

Olivier 1804, II, p. 39, pl. 31, fig. 1. Type locality: Lake Mareotis, Egypt. One syntype, lake Mareotis. Referred to *Pila Röding* 1798 by Brown (1980, p. 44). Distribution: Northern and eastern Africa.

*ovularis* Olivier 1801, *Bulimus*. pl. 5, fig. 10

Olivier 1801, I, p. 225, pl. 17, figs. 12a, b. Type locality: given as Gemlik, Turkey. Thirteen syntypes, labelled as coming from Mossul, but inventoried by Valenciennes in 1819 as coming from Gemlik. Type species of *Jaminia (Multidentula)* Lindholm 1925. Distribution: Turkey, Syria, Israel.

*retusus* Olivier 1801, *Bulimus* pl. 6, fig. 11

Olivier 1801, I, p. 416, pl. 17, figs. 2a, b. Type locality: Crete. Fifteen syntypes, one lot of five and one of ten, Standie (=Dia, Crete). Referred to *Albinaria* Vest 1867 by Nordsieck (1977, p. 305). Distribution: Crete.

*spiri plana* Olivier 1801, *Helix*. pl. 6, figs 3 and 6

Olivier 1801, I, p. 415, pl. 17, figs. 7a, b, c. Species based on specimens from Crete and Rhodes. Nine syntypes, three lots of seven, one, and one shell respectively, labelled Rhodes, and seemingly containing two species. Only two specimens, one adult and one juvenile, fit the original figures and these are figured here. Type species of *Levantina* Kobelt 1871. Distribution: Rhodes, Kalymnos.

*teres* Olivier 1801, *Bulimus*. pl. 6, fig. 7

Olivier 1801, I, p. 417, pl. 17, figs. 6a, b. Type locality: Crete. Four syntypes, Standie (=Dia, Crete). Referred to *Albinaria* Vest 1867 by Nordsieck (1977, p. 306). Distribution: Crete.



*tigridis* Bourguignat 1852, *Unio*. pl. 7, fig. 3

Bourguignat 1852, p. 30, 1853, p. 77, pl. 4, figs. 7–9. Type locality: Baghdad, Iraq. One valve, Baghdad, probable holotype; although Bourguignat figured two valves, it is quite probable that he extrapolated the missing one. Retained in *Unio* Philipsson 1788 by Germain (1922, p. 32). Distribution: Middle East.

*torticollis* Olivier 1801, *Bulimus*. pl. 5, fig. 9

Olivier 1801, I, p. 416, pl. 17, figs. 4a, b. Type locality: Crete. Fifteen syntypes, in two lots of eight and seven shells respectively, Standia (=Dia, Crete). Referred to *Albinaria* Vest 1867 by Nordsieck (1977, p. 306). Distribution: Crete.

*tripolitanus* Bourguignat 1852, *Unio*. pl. 7, fig. 4

Bourguignat 1852, p. 28; 1853: 75, pl. 4, figs. 10–12. Type locality: Tripoli, Lebanon. Probable holotype, figured by Bourguignat. Germain (1922, p. 7) suggests that *tripolitanus* is perhaps only a form of *Leguminaia* (*Leguminaia*) *mardinensis* (Lea 1864).

*unicolor* Olivier 1804, *Cyclostoma*. pl. 5, fig. 6

Olivier 1804, II, p. 39, pl. 31, figs. 9a, b. Type locality: Kalidje, Egypt. Three syntypes, canals of Egypt. Type species of *Bellamya* Jousseau 1886. Distribution: Northern and central Africa.

*zebra* Olivier 1801, *non* Bruguière 1792, *Bulimus*. pl. 5, fig. 5

Olivier 1801, I, p. 225, pl. 17, fig. 10a, b. Type locality: Gemlik, Turkey. Eight syntypes, Gemlik. Preoccupied by *Bulimus zebra* Bruguière 1792, and renamed *Helix zebrula* by Férussac (1821, p. 70). Type species of *Chondrus* Cuvier 1817. Distribution: Greece, Aegean Islands, Turkey.

*zebrula* Férussac 1821, *Helix*, pl. 5, fig. 5

Férussac 1821, p. 70. *nom. nov.* for *Bulimus zebra* Olivier 1801, *non* Bruguière 1792.

#### PLATE 5

Fig. 1. *Pila ovata* (Olivier), syntype (H=64 mm). Fig. 2. *Melanoides fasciolata* Olivier, syntype (H=21.5 mm). Fig. 3. *Lanistes carinata* (Olivier), syntype (D=35.5 mm). Fig. 4. *Planorbis orientalis* Olivier, probable syntype (D=10.7 mm). Fig. 5. *Chondrus zebrula* (Férussac), syntype (H=17 mm). Fig. 6. *Bellamya unicolor* (Olivier), syntype (H=23 mm). Fig. 7. *Cleopatra bulimoides* (Olivier), syntype (H=8.2 mm). Fig. 8. *Zebrina fasciolata* (Olivier), syntype from Rhodes (H=22.8 mm). Fig. 9. *Albinaria torticollis* (Olivier), syntype (H=12 mm). Fig. 10. *Jaminia* (*Multidentula*) *ovularis* (Olivier), syntype (H=6 mm). Fig. 11. *Melanopsis buccinoidea* (Olivier), probable syntype (H=29 mm). Fig. 12. *Lacinaria* (*Denticularia*) *denticulata* (Olivier), syntype? from the mixture including the type series, from Khios or Gemlik (cf. Pl. 2 Fig. 10). H=14.5 mm.

#### PLATE 6

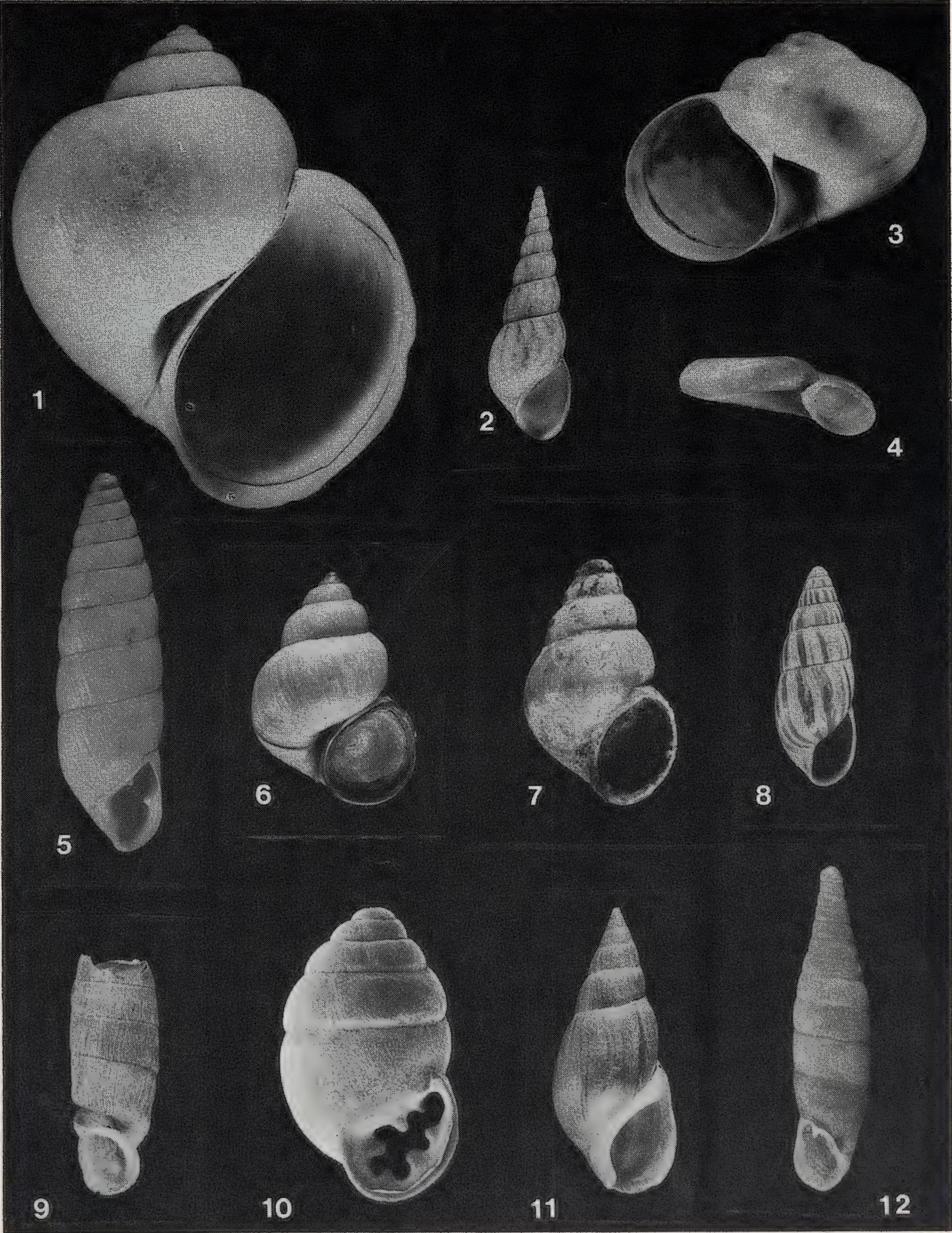
Fig. 1. *Helix mahometana* Bourguignat=*Helix castanea* Olivier *non* Müller, probable syntype (H=41.5 mm). Fig. 2. *Levantina* (*Assyriella*) *guttata* (Olivier), syntype (D=33.5 mm). Fig. 3. *Levantina spiriplana* (Olivier), adult syntype (see also Fig. 6). D=30 mm. Fig. 4. *Trochoidea* (*Xeroptyca*) *crenulata* (Olivier) (*non Helix crenulata* Müller), syntype (D=12.3 mm). Fig. 5. *Sphincterochila* (*Rima*) *cariosa* (Olivier), syntype (D=19.5 mm). Fig. 6. *Levantina spiriplana* (Olivier), juvenile syntype depicted by Olivier (D=21.5 mm) (see also Fig. 3). Fig. 7. *Albinaria teres* (Olivier), syntype (H=21.6 mm). Fig. 8. *Albinaria inflata* (Olivier), 'elongated' syntype (H=22.8 mm). Fig. 9. *Albinaria inflata* (Olivier), 'inflated' syntype (H=17.8 mm). Fig. 10. *Lacinaria* (*Denticularia*) *denticulata* (Olivier), syntype? from the mixture including the type series (cf. Pl. 5 Fig. 12). (H=16.2 mm). Fig. 11. *Albinaria retusa* (Olivier), syntype (H=14.4 mm).

#### PLATE 7

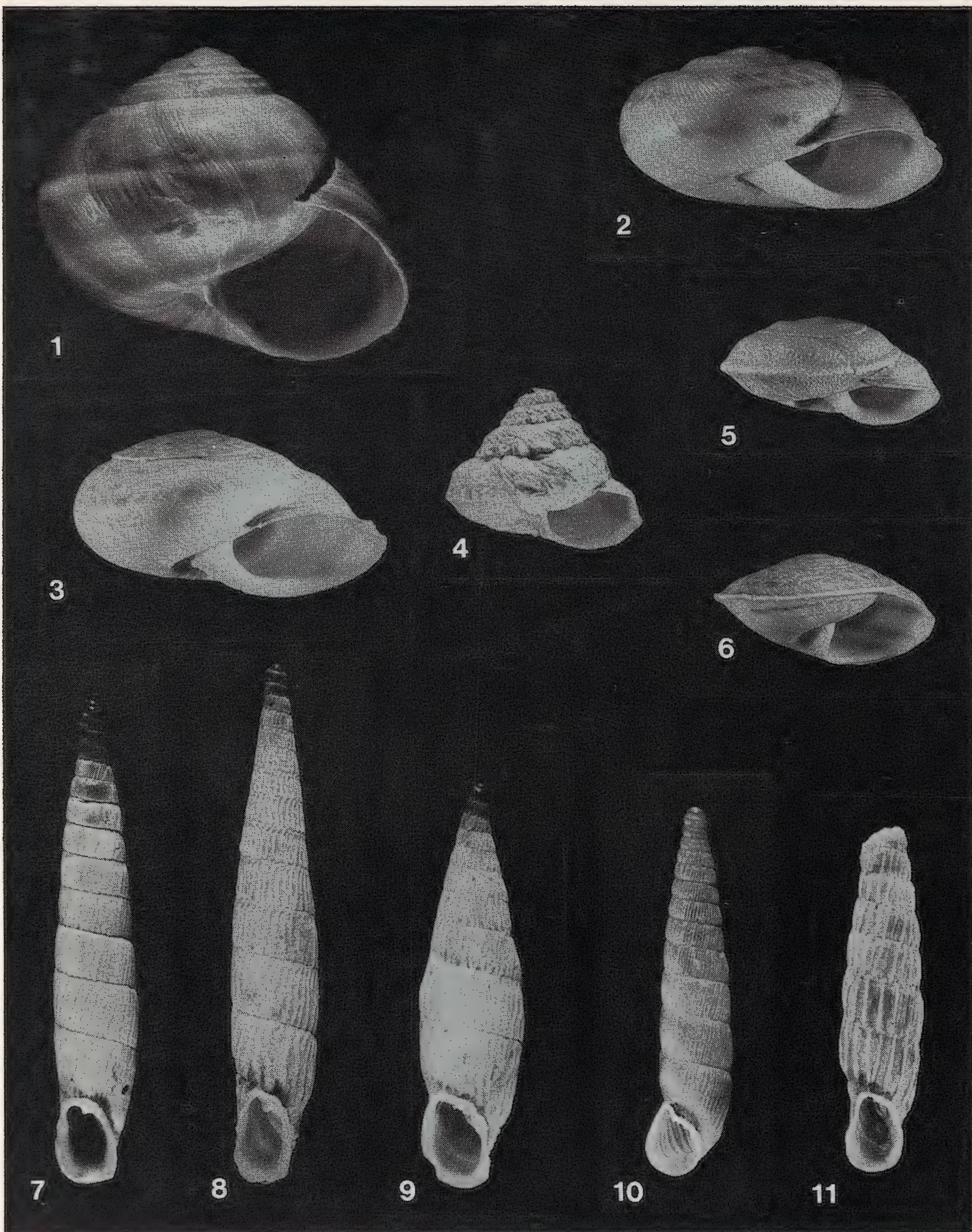
Fig. 1. *Leguminaia* (*Pseudodontopsis*) *euphratica* (Bourguignat), probable holotype (length=70 mm). Fig. 2. *Unio bagdadensis* Bourguignat, probable holotype (length=57.5 mm). Fig. 3. *Unio tigridis* Bourguignat, probable holotype (length=59.6 mm). Fig. 4. *Leguminaia* (*Leguminaia*) *tripolitana* (Bourguignat), probable holotype (length=70.6 mm). Fig. 5. *Unio bruguierianus* Bourguignat=*Unio orientalis* Bourguignat *non* Lea, figured syntype (length=48 mm).

Photos by A. Foubert

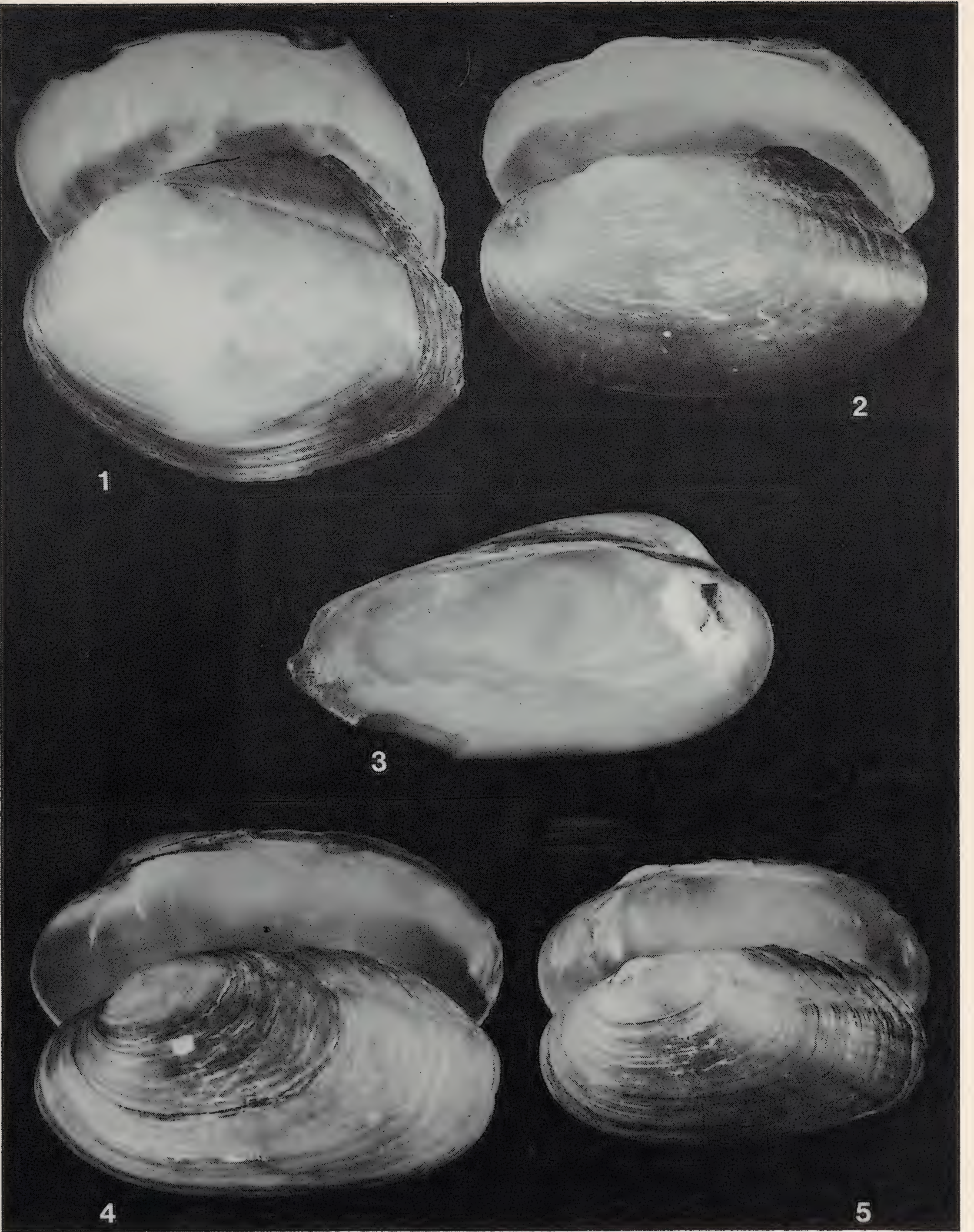














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- , 1804. *Idem*, Tome second. Agasse, Paris: 466 pp. Atlas, 2d livraison: VII pp., pl. 18–32.
- , 1807. *Idem*, Tome troisième. Agasse, Paris, 566 pp. Atlas, 3d livraison: VIII pp., pl. 34–50.
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# MARINE MOLLUSCA DESCRIBED BY W. TURTON AND W. CLARK

ANDERS WARÉN\*

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*Abstract:* A list is given of the marine Mollusca described by the two 19th century authors W. Turton and W. Clark, with comments on the present status of the names. Still existing type material is listed. Short biographies and bibliographies are included.

## INTRODUCTION

It is well known that the Jeffreys collection, including the types of most of the species described by Jeffreys was purchased by the Smithsonian Institution Washington D.C. in 1882, but it is less well known that this collection also contained other type material (Warén 1980, Bartsch 1946). In the present paper I deal with the types of two earlier British authors, William Turton and William Clark, whose collections were acquired by Jeffreys, and are included in the collections of the U.S. National Museum of Natural History (USNM), Division of Molluscs.

Not very much is known about how or when these two collections were acquired by Jeffreys, but judging from Jeffreys' remarks on the names of Turton in 'British Conchology' (Jeffreys 1862–69) the vast majority of the Turton collection was available to him when he wrote 'British Conchology'. The same was presumably also the case with the Clark collection. During the present study it has been possible to locate only a small number of the types, and it is unlikely that more will be found. I suppose that Jeffreys kept only parts of the collections, presumably groups like rissoids, pyramidellids etc., in which he was especially interested and probably also monstrous or deviating specimens. Nevertheless, Jeffreys had an opportunity to examine the type specimens and I believe his synonymies to be, therefore, more well founded than any subsequent re-evaluation, which is not based on actual type specimens, could be. For that reason I suggest that for the numerous species, implicitly described by Turton of which there are no types left, the best solution is to follow the identifications by Jeffreys. If it proves necessary to select neotypes of such species I would recommend that the specimen figured by Jeffreys in 'British Conchology' for the corresponding name be selected. (They are easily identified in the collection by being marked 'Figd. type Brit. Conch.'). Such a procedure will contribute to a stabilized nomenclature.

The lots here considered to be types were usually labelled with Turton's or Clark's names, the locality from where the species was described and 'Turton' or 'Clark'. In a few cases some of this information was not present on the label but the identity of the specimens could be verified by comparison with the original description. (All the Jeffreys collection was relabelled when it was catalogued at USNM and no original labels were saved.)

When no specimens with locality or collector information corresponding to the species could be found the types are presumed to be lost. It is possible that some of these 'lost' types may appear in some other museum collection, probably via one or several amateur collections, but for example British Museum (Nat. Hist.) does not have any specimens that can be suspected of being Clark or Turton types.

In the following parts of this paper I give a short biographic sketch, a list of molluscan papers and a list of the marine mollusca described by the two authors. In the lists I give the

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type locality, type material and the presently accepted systematic position of the name. A black dot in front of a generic or specific name indicates that it is the presently accepted or valid name for the taxon.

## WILLIAM CLARK

I have not been able to obtain any information about the life of W. Clark, except that which can be derived from his published papers.

Clark published his first paper in 1828, a description of the animals of some cephalaspid. He did not resume publishing until 1849. From that year onwards he published numerous papers in *Annals and Magazine of Natural History* and in 1855 he published a book, 'British marine testaceous Mollusca'. He lived at Norfolk Crescent, Bath but from 1810 he spent many summers in Exmouth.

When Clark published his work on the British Mollusca (1855a) he was evidently quite an old man because he remarks: 'It would be almost presumptuous of me to calculate upon being able to watch the publication of my observations during such a long period as four years'. Nevertheless he survived that period of time because his last paper was published in 1860.

Clark described seven new species and one new genus. Only four of his names are still valid, but he will be remembered for his accurate and detailed descriptions of the soft parts of British molluscs, especially the minute species, on which Forbes & Hanley (1848-53) and Jeffreys (1860-69) based their descriptions. This interest in the soft parts often made Clark draw too far-reaching conclusions about relations and classification of a group, because he did not examine the internal anatomy and radulae to any great extent. This was also the reason for a scathing criticism (Anonymous 1855) of his book (Clark 1855a). Clark also disagreed widely with the leading British conchologist of his time, J. G. Jeffreys, which can be seen in most of his papers, and especially in Clark 1859b.

## MALACOLOGICAL PUBLICATIONS BY W. CLARK

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- 1849a. Observations on the animal of *Kellia rubra*. *Ann. Mag. nat Hist.* (2) **3**: 292-295; (2) **3**: 452-456; (2) **4**: 142-146.
- 1849b. Observations on the recent foraminifera. *Ibid.* (2) **3**: 380-383.
- 1849c. On the animals of *Caecum trachea* and *C. glabrum*. *Ibid.* (2) **4**: 180-184.
- 1849d. On the animal of *Dentalium tarentinum*. *Ibid.* (2) **4**: 321-330.
- 1849e. On two new species of testaceous Mollusca. *Ibid.* (2) **4**: 424-425.
- 1850a. On the terebrating Mollusca. *Ibid.* (2) **5**: 6-14.
- 1850b. On the recent foraminifera. *Ibid.* (2) **3**: 161-171.
- 1850c. Observations on the Littorinidae. *Ibid.* (2) **5**: 352-364.
- 1850d. Observations on the Lacunae. *Ibid.* (2) **6**: 29-35.
- 1850e. Observations on the animals of the Bullidae. *Ibid.* (2) **5**: 98-108.
- 1850f. On the Pholadidae. *Ibid.* (2) **6**: 314-336.
- 1850g. On the Convolvulidae, Tornatellidae and Pyramidellidae. *Ibid.* (2) **6**: 444-464.
- 1851a. On the Muricidae. *Ibid.* (2) **7**: 109-129.
- 1851b. On a new species of *Chemnitzia*. *Ibid.* 129-130.
- 1851c. On *Ancylus oblongus* and *A. fluviatilis*. *Ibid.* 278-285.
- 1851d. On the *Chemnitzia opalina* and *C. diaphana*. *Ibid.* (2) **7**: 292-297.
- 1851e. On the Chemnitziae. *Ibid.* (2) **7**: 380-394.
- 1851f. On the classification of the British Marine testaceous Mollusca. *Ibid.* (2) **7**: 469-480.
- 1851g. On the Skeneadae. *Ibid.* (2) **8**: 44-49.
- 1851h. Further observations on the Chemnitziae. *Ibid.* (2) **8**: 108-113.
- 1852a. On a new British species of *Lepton*. *Ibid.* (2) **9**: 191-192.



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- 1852b. Further observations on *Lepton clarkiae*. *Ibid.* (2) **9**: 293–294.
- 1852c. On the *Venus undata* of authors. *Ibid.* (2) **9**: 400–402.
- 1852d. On some of the rarer British gasteropodous Mollusca. *Ibid.* (2) **10**: 22–23.
- 1852e. On the genus *Lepton*. *Ibid.* (2) **10**: 129–134.
- 1852f. On the animals of the Chemnitziae which have not been described. *Ibid.* (2) **10**: 195–210.
- 1852g. On some undescribed animals of the British Rissoae. *Ibid.* (2) **10**: 254–263.
- 1853a. On the Ianthinae, Scalariae, Naticae, Lamellariae and Velutinae. *Ibid.* (2) **11**: 44–58.
- 1853b. On the Chitonidae. *Ibid.* (2) **11**: 274–283.
- 1853c. On the genus *Truncatella*. *Ibid.* (2) **12**: 4–8.
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- 1859a. On the British *Trochus cutlerianus* (Clark) being the *Skenea cutleriana* of the ‘British Mollusca’ and on the *Trochus exilis* of Philippi. *Ibid.* (3) **3**: 192–195.
- 1859b. On Mr. Jeffreys’s ‘Gleanings in British Conchology’. *Ibid.* (3) **3**: 406–414.
- 1860. On the *Lepton sulcatulum* of Mr. Gwyn Jeffreys. *Ibid.* (3) **5**: 27–29.

## GENERA DESCRIBED BY W. CLARK

*Barleeia* Clark 1855a, p. 391. Type species: *Turbo rubrum* J. Adams 1797, (= *Barleeia unifasciata* (Montagu 1803)), by monotypy. (*Turbo rubrum* J. Adams is preoccupied by *T. rubrum* C. U. von Salis 1793)

## SPECIES DESCRIBED BY W. CLARK

- barleei*/*Chemnitzia*/Clark 1851b, p. 446. Type locality: Shetland Islands (N Great Britain). Type material: Lost. Clark described this as a new species, although he listed *Rissoa eximia* Jeffreys 1848 as a synonym.
- branscombi*/*Fusus*/Clark 1849e, p. 425. Type locality: Coralline zone, Exmouth, Devon, (Great Britain). Type material: Lost. This is *Comarmondia gracilis* (Montagu) (Jeffreys 1867, p. 365).
- *clarkiae*/*Lepton*/Clark 1852a, p. 191. Type locality: ‘Zonam corallinam Devoniae Meridionalis, propae ostium Islae rarius habitat’ (S Great Britain). Type material: Three syntypes (complete specimens) USNM 199440. This is *Epilepton clarkiae*. Plate 8, figs 1–2.
- *cutlerianus*/*Trochus*/Clark 1849e, p. 424. Type locality: Coralline zone of Exmouth, Devon, (S Great Britain). Type material: Lost. This is *Skenea cutleriana* Clark. Clark (1850, p. 364) remarked that this species is very close to *Delphinula elegantula* Philippi.
- *gulsonae*/*Chemnitzia*/Clark 1850g, p. 459. Type locality: Exmouth, South Devon, (Great Britain), 13 fathoms. Type material: Lost. This is *Pherusa gulsonae* (Clark).
- intermedia*/*Anatina*/Clark 1855a, p. 141. New name for *Anatina villosiuscula* (*Thracia villosiuscula* (MacGillivray)). Clark used this old manuscript name, claiming that it had been well-known for 30 years, along the Devon Coast, although he was aware that there was an available, published name for it.
- *pruniosa*/*Bulla*/Clark 1828, p. 339. Type locality: Budleigh Salterton, Devon, (S Great Britain). Type material: One syntype, USNM 176645. This is *Philine pruniosa* (Clark). Plate 1, fig. 3.



## NEW FAMILY NAMES INTRODUCED BY W. CLARK

Montacutidae Clark 1855a, p. 94.

Turtonidae Clark 1855a, p. 96.

Clark also introduced the two families Peloridae (1855a, p. 469) and Heterophrosynidae (1855a, p. 387), but they were not based on a certain genus and contain each a disparate array of Mesogastropoda. The family name Barleeidae has sometimes been ascribed to Clark (sometimes also Thiele) but was introduced by J. E. Gray (Jeffreys 1867, p. 55).

## WILLIAM TURTON 1762–1835

Not very much is known about the life of W. Turton. Most of the information below originates from Dean (1936), some fragments originate from comments by Jeffreys, Clark and others. Some further details without malacological interest can be found in the *Dictionary of National Biography*.

Turton lived in Swansea during the period 1791–1807, then in Dublin, Teignmouth, Torquay and Bideford. He was a physician and published several papers on medical topics such as 'hot and cold baths', 'consumption' and a medical dictionary. He even published a series of poems in English, Greek and Latin, commemorating Lord Nelson. The main topic of his writing activities, however, was natural sciences, especially conchology. In all Turton published 17 new genera and 109 new specific names, of which 14 generic and 16 specific names are still considered valid.

The collection of Turton was acquired by W. Clark some time before 1831 (cf Turton 1831 and Clark 1855a, p. 36).

As was the habit in his days, Turton was not a very critical worker, which is indicated by the low percentage (12) of his specific names that still are considered valid and the fact that several of his species described as British are native in other parts of the world. Clark (1855a, p. 37) wrote: 'The fact is, that Dr. Turton was a man of great simplicity, and so far from age giving an increase of caution, it appears, with him, to have had a contrary effect; if it were necessary, I could relate several curious and laughable stories of his being duped by the frauds of crafty shell-dealers'. And Jeffreys (1865, p. 183) wrote: 'He may have been like Bellario "A learned Doctor" each in his own profession; and we will charitably think that the physician understood the constitution of his patients better than that of the *Teredo*'.

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- 1807. *British fauna, containing a compendium of the zoology of the British Islands: According to the Linnean system*. Swansea. Vol. 1. (All published.) (Cf. Winckworth 1945).
- 1816. Irish Conchology. *Dublin Examiner* **1**: 230–240.
- 1819. *A conchological dictionary of the British Islands*. J. Booth, London. 272 pp.
- 1822. *Conchylia Insularum Britannicarum*. M. A. Nattali, London. 280 pp.
- 1825. Description of new British shells. *Zool. Journ.* **2**: 361–367.
- 1827. On the genus *Lacuna*. *Zool. Journ.* **3**: 190–192.
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## GENERA DESCRIBED BY W. TURTON

*Agina* Turton 1822, p. XIII, 54. Type species: *Mya purpurea* Montagu, by monotypy (= *Turtonia minuta* (Fabricius)). Turton's figure of what he believed to be *Mya purpurea* Montagu clearly shows a specimen of *Hiatella*, while Montagu's species is what now is generally called *Turtonia minuta* (Fabricius). The genus *Agina* is thus based on a misidentified type species and the case has to be brought to the I.C.Z.N. The name *Agina*, however, has universally been accepted as a junior synonym of *Hiatella* and *Turtonia* is as well established so any change would cause unnecessary confusion.

*Cryptodon* Turton 1822, p. 121. Type species: *Tellina flexuosa* Montagu, by monotypy. *Thyasira* Lamarck 1819, has the same type species and is in common use.

● *Ervilia* Turton 1822, p. 55. Type species: *Mya nitens* Montagu, by monotypy.

● *Galeomma* Turton 1825, p. 361. Type species: *Galeomma turtoni* Sowerby, by monotypy.

● *Goodallia* Turton 1822, p. 76. Type species: *Mactra triangularis* Montagu, subsequent designation by Herrmannsen 1847.

● *Kellia* Turton 1822, p. 56. Type species: *Mya suborbicularis* Montagu, subsequent designation by Herrmannsen 1847.

● *Lacuna* Turton 1827, p. 190. Type species: *Helix lacuna* Montagu (= *Lacuna parva* (Da Costa)), by tautonymy.

● *Lepton* Turton 1822, p. 61. Type species: *Solen squamosus* Montagu, subsequent designation by Herrmannsen 1847.

*Listera* Turton 1822, p. 50. Type species: *Mactra compressa* Pulteney (*Scrobicularia plana* (Da Costa)), by monotypy. *Scrobicularia* Schumacher 1817, was described five years before *Listera* and was based on the same species so *Listera* becomes a junior synonym.

● *Lyonsia* Turton 1822, p. 34. Type species: *Mya striata* Montagu (= *Lyonsia norwegica* (Gmelin)), by monotypy.

● *Montacuta* Turton 1822, p. 58. Type species: *Ligula substriata* Pennant, subsequent designation by Herrmannsen 1847.

● *Myrtea* Turton 1822, p. 133. Type species: *Venus spinifera* Montagu, by monotypy.

● *Pholadidea* Turton 1819, p. 147. Type species: *Pholadidea loscombiana* Turton, by monotypy.

● *Sphaenia* Turton 1822, p. 36. Type species: *Sphaenia binghami* Turton, subsequent designation by Gray 1847.

● *Strigilla* Turton 1822, p. 117. Type species: *Tellina carnaria* Linnaeus, subsequent designation by Herrmannsen 1847.

● *Tornus* Turton in Turton & Kingston 1830, no pagination. Type species: *Helix subcarinata* Montagu, by monotypy.

● *Xylophaga* Turton 1822, p. 253. Type species: *Teredo dorsalis* Turton, by monotypy.

## MARINE SPECIES DESCRIBED BY W. TURTON

*aenea/Venus*/Turton 1819, p. 248. Type locality: Blue clay at Clontarf, near Dublin, Ireland. Type material: USNM 200 891, 2 complete specimens, 1 single valve. As pointed out by Jeffreys (1864, p. 351), this is a form of *Venerupis aurea* (Gmelin).

*alba/Bulla*/Turton 1825, p. 364. Type locality: British Channel. Types lost. Jeffreys (1867, p. 364) considered this a synonym of *Bulla striata* Brugiere.

*alba/Lucina*/Turton 1822, p. 114. Type locality: British Channel and shores about Guernsea (Guernsey). Types lost. 'The types of Turton's *Lucina alba* is composed of two odd much-worn valves of *L. borealis*' (Jeffreys 1864, p. 255).

*alba/Voluta*/Turton 1819, p. 250. Type locality: Dublin Bay (Ireland) and North Britain.



Type material: 1 Syntype USNM 55326. This is *Leucopepla bidentata* (Montagu) (Jeffreys 1864, p. 255).

*antiqua/Venus/Turton* 1816, p. 234 (nomen nudum).

*albulus/Turbo/Turton* 1802. New name for *Turbo albus* J. Adams 1797, not Pennant 1777.

*album/Dentalium/Turton* 1819, p. 256. New name for *D. eburneum* Turton 1819. Jeffreys (1865, p. 198) considers this to be *D. variabile* Deshayes.

● *ascaris/Turbo/Turton* (1816, p. 238, nomen nudum) 1819, p. 217. Type locality: Seafield, Ireland. Type material: Lost.

*bifidus/Mytilus/Turton* 1816, p. 235. Nomen nudum.

● *binghami/Sphaenia/Turton* 1822, p. 37. Type locality: In rocks, Torbay (S Great Britain). Type material: Lectotype USNM 171 240, several paralectotypes, USNM 679166, selected by Hanks (1969). Plate 10, figs 1–4.

● *bipennata/Teredo/Turton* 1819, p. 184. Type locality: In fir timber, River Ex, Devonshire, Great Britain. Type material: Lectotype USNM 194256, selected by Turner (1966, p. 91).

*bullata/Lima/Turton* 1822, p. 218. Validation of a nonbinominal name of Chemnitz (1784, p. 348), but this name is pre-occupied by *Lima bullata* Lamarck 1807.

*carinatum/Buccinum/Turton* 1819, p. 13. Type locality: Dublin; Portmarnock; Bray (Ireland), Exmouth (S Great Britain). Type material: Syntype USNM 191926 (Between Berry Head and Exmouth). This is a carinated monstrosity of *Buccinum undatum* Linnaeus.

*chordula/Murex/Turton* 1819, p. 94. Type locality: Dublin (Ireland). Type material: Two syntypes USNM 190864. This is the young of '*Pleurotoma*' *rufa* (Montagu) (Jeffreys 1869, p. 394).

*chrysalis/Turbo/Turton* 1819, p. 221. Type locality: Sandbanks at Portmarnock, Ireland, rejectments of rivers in England. This is *Pupa marginata* (Jeffreys 1861, p. 252).

*cingulum/Patella/Turton* 1802. New name for *Patella melanozonias* Gmelin.

*clausum/Dentalium/Turton* 1819, p. 39, Type locality: Calves Island, W Ireland. Type material: Holotype USNM 174999. This is the lower part of a quill of a birds feather. (Jeffreys 1865, p. 198).

● *costulata/Psammobia/Turton* 1822, p. 87. Type locality: Dredged in Torbay and the Channel (British). Type material: Two syntypes USNM 178601. Plate 9, figs 1–4.

*crassa/Mactra/Turton* 1822, p. 69. Type locality: Irish Channel. Type material: Lost. This is *Spisula solida* (Brown) (Jeffreys 1864, p. 69).

● *deaurata/Mactra/Turton* 1822, p. 71. Type locality: Dredged up in the offing of Exmouth (England). Type material: Holotype USNM 172665. This species originates from New Foundland (Jeffreys 1864, p. 414 and Davis 1965, p. 96–100).

*dentata/Patella/Turton* 1802. New name for *P. denticulata* Gmelin.

*dentatus/Mytilus/Turton* 1819, p. 115. Type locality: Bog of Allen, Ireland. This is *Anodonta cygnea* (Linnaeus) (Jeffreys 1861, p. 42).

*diclavis/Solen/Turton* 1819, p. 164. Type locality: Scilly (Islands, S British Channel). Type material: Holotype USNM 171268. This is *Tagelus plebeius* (Lightfoot) (Jeffreys 1865, p. 8).

● *dorsalis/Teredo/Turton* 1819, p. 185. Type locality: Devonshire Coast, Great Britain. Type material: Lost. This is *Xylophaga dorsalis* (Turton).

*eburneum/Dentalium/Turton* 1819, p. 34. Type locality: Western Coast (Great Britain). Type material: Lost. Cf. *D. album*.

*elliptica/Helix/Turton* 1816, p. 239. Nomen nudum.

*explanata/Patella/Turton* 1802, New name for *P. depressa* Gmelin, not Pennant.

*extinctorium/Patella/Turton* 1819, p. 138. Type locality: From '*Serpula tubularia*', Torbay, S Great Britain. Type material: Lost. This is the operculum of a polychete (Jeffreys 1865, p. 235).

*fabalis/Turbo/Turton* 1825, p. 366. Type locality: Rocks at Scarborough, (S Great Britain). Type material: Seven syntypes USNM 185758. This is a form of *Littorina littoralis* (Linnaeus) (Jeffreys 1865, p. 357).



- *fenestratus/Fusus*/Turton 1834, p. 351. Type locality: Cork (Ireland). Type material: Holotype USNM 192347. This is *Turrisipho fenestratus* (Turton). Plate 8, fig. 6.
- florida/Psammobia*/Turton 1822, p. 86. Type locality: W Great Britain and Ireland. Type material: Lost. This is *Gari tellinella* (Lamarck) (Jeffreys 1864, p. 394).
- fusiformis/Voluta*/Turton 1819, p. 251. Type locality: Sands at Exmouth (S Great Britain). 'The type is *Marginella laevis*' (= *Erato voluta* (Donovan)) (Jeffreys 1867, p. 402).
- gibbsi/Modiola*/Turton 1822, p. 200. Type locality: Western Coasts (Great Britain). Type material: Lost. Jeffreys wrote (1864, p. 116): '*Modiolus gibbsi* Leach is *M. barbatus*'. I do not know if that is true also for Turton's species.
- glabra/Mactra*/Turton 1816, p. 234. Nomen nudum.
- glabra/Patella*/Turton 1802. New name for *Patella inaequalis* Gmelin.
- graphicus/Turbo*/Turton 1816, p. 238. Nomen nudum.
- hyalina/Bulla*/Turton 1834, p. 353, Type locality: Newcastle and Lands End in Cornwall (Great Britain). Type material: Lost. This is *Diaphana minuta* (Brown).
- imbricata/Patella*/Turton 1802. New name for *P. antiquata* Gmelin.
- labiatum/Dentalium*/Turton 1819, p. 38. Type locality: Torbay (S Great Britain). Type material: Six syntypes USNM 174971. This is *Dentalium tarentinum* Lamarck (Jeffreys 1865, p. 196).
- laeve/Dentalium*/Turton 1819, p. 256. Type locality: Torbay (S Great Britain). Type material: Five syntypes USNM 174969. This is *D. tarentinum* Lamarck (Jeffreys, 1865, p. 196).
- laeviusculum/Buccinum*/Turton, 1802. New name for *Buccinum laeve* Gmelin, not J. Adams.
- lamellata/Pholas*/Turton 1822, p. 4. Type locality: Exmouth and Torbay (S Great Britain). Type material: Lost. This is the young of *Pholadidea loscombiana* Turton (Jeffreys 1865, p. 118).
- leucoma/Lucina*/Turton 1822, p. 113. Type locality: Torbay, British Channel and Guernsea (S Great Britain). Type material: Lost. 'Scarcely a variety of *Loripes lacteus*' (Jeffreys 1864, p. 234).
- ligula/Solen*/Turton 1822, p. 81. Type locality: Sands in Torbay (S Great Britain). Type material: Lost. This is *Ensis siliqua* (Linnaeus) (Jeffreys 1865, p. 19).
- lineata/Tellina*/Turton 1819, p. 168. Type locality: Torbay (S Great Britain). Type material: Several syntypes USNM 178267. This is *Tellina pygmea* Loven. (Jeffreys 1864, p. 390). Turton's name is older than the one presently in use, but should probably be regarded as a *Nomen Oblitum*. Plate 10, figs 5–8.
- *loscombiana/Pholadidea*/Goodall MS, Turton 1819, p. 147. Type locality: Exmouth (S Great Britain). Type material: Lost.
- maculata/Tellina*/Turton 1819, p. 173. Type locality: Bantry Bay (Ireland). Type material: Lost. 'Certainly *Tellina crassa* Pennant' (Jeffreys 1864, p. 375).
- *malleolus/Teredo*/Turton 1822, p. 255. Type locality: From timber in Torbay (S Great Britain). Type material: Lectotype USNM 194213 (Turner 1965, p. 109.) This is *Teredora malleolus* (Turton).
- minima/Arca*/Turton 1819, p. 8. Type locality: Devonshire (S Great Britain). Type material: Lost. This is *Glycymeris glycymeris* (Linnaeus) (Jeffreys 1864, p. 169).
- minimum/Buccinum*/Turton 1802. New name for *Buccinum minutum* Pennant, not J. Adams. This is *Nassarius incrassatus* (Strom) (Jeffreys 1867, p. 314).
- monilis/Turbo*/Turton 1819, p. 200. Type locality: Exmouth (S Great Britain). Type material: Lost. This is *Alvania carinata* (Da Costa) (Jeffreys 1867, p. 7).
- montacuti/Lacuna*/Turton 1827, p. 119. New name for *Helix lacuna* Montagu (*Lacuna parva* Da Costa).
- montacuti/Venus*/Turton 1819, p. 243. New name for *Venus compressa* Montagu (= *Astarte montagui* (Dillwyn)).
- nana/Teredo*/Turton 1822, p. 16. Type locality: Wood from Torbay (Great Britain). Type material: Syntypes USNM 194258. Forbes & Hanley (1853 p. 77) changed the name to *megotara*, a now well-known name. Turner (1966, p. 112) considered the syntypes of *nana*



unidentifiable, and selected a neotype of *megotara* in BMNH, which is not correctly done, because a replacement name takes the types of the name replaced. Any change here will, however, increase confusion.

*naassensis/Helix*/Turton 1816, p. 239. Nomen nudum.

*nitens/Venus*/Turton 1819, p. 247. Type locality: In the blue clay of Clontarf, Ireland. Type material: Lost. Jeffreys (1864, p. 351) considered this a form of *Venerupis aurea* (Gmelin).

● *nitidum/Lepton*/Turton 1822, p. 63. Type locality: Coralline in Tenby (S Great Britain). Type material: Lost.

*nodosa/Patella*/Turton 1802. New name for *Patella nodulosa* Gmelin.

*nucleus/Corbula*/Turton 1822, p. 39. New name for *Tellina inaequivalvis* Pennant, not Linnaeus. This is *Corbula gibba* (Olivi).

*oblonga/Montacuta*/Turton 1822, p. 61. Type locality: From sand in Torbay (S Great Britain). Type material: Lost. This is *Montacuta ferruginosa* (Montagu) (Jeffreys 1864, p. 212).

*oblonga/Hiatella*/Turton 1822, p. 25. Type locality: Dublin Bay (Ireland) and Torbay (S Great Britain), in rocks. Type material: Lost. This is *Hiatella* sp.

*ovalis/Mya*/Turton 1822, p. 33. Type locality: Dublin Bay at Clontarf (Ireland). Type material: Holotype USNM 196927. This is a young *Mya truncata* Linnaeus (Jeffreys 1865, p. 70).

*ovata/Patella*/Turton 1802. New name for *Patella depressa* Gmelin.

● *ovum/Buccinum*/Turton 1825, p. 366. Type locality: Off Plymouth. Jeffreys (1867) suspected this type locality to be wrong and that the specimen actually came from Cork (Ireland). Type material: Holotype USNM 192257. This is *Liomesus ovum* (Turton). Plate 8, fig. 5.

● *otis/Helix*/Turton 1819, p. 70. Type locality: Devonshire (S Great Britain). Type material: Six syntypes USNM 55335. This is *Otina otis* (Turton).

*pallida/Venus*/Turton 1822, p. 150. Type locality: Dawlish (Great Britain). Type material: Lost. 'The types are doctored specimens of *Venus gallina* Linnaeus' (Jeffreys 1864, p. 348).

*papyracea/Pholas*/Turton 1822, p. 2. Type locality: Torbay (S Great Britain). Type material: Lost. This is *Pholadidea loscombiana* (fide Turton, 1822, p. 2).

*parasitica/Ostrea*/Turton 1819, p. 134. Type locality: Devonshire and Ireland. Type material: Syntype USNM 196880. 'A variety of *Ostrea edulis* Linnaeus' (Jeffreys 1864, p. 38).

*pellucida/Nerita*/Turton 1816, p. 240. Nomen nudum.

#### PLATE 8

Figs 1–2. *Lepton clarkiae*, syntype. USNM 199440. 1.4 mm. Fig. 3. *Bulla pruniosa*, holotype. USNM 176645. 6 mm. Fig. 4. *Phasinella styliifera*, lectotype. USNM 177239. 2.8 mm. Fig. 5. *Buccinum ovum*, holotype. USNM 192257. 41 mm. Fig. 6. *Fusus fenestratus*, holotype. USNM 192347. 30 mm. Fig. 7. *Pleurotoma trevillianum*, lectotype. USNM 190860. 9 mm.

#### PLATE 9.

Figs 1–4. *Psammobia costulata*, syntypes. USNM 178601. 23 mm. Figs 5–8. *Galeomma turtoni*, syntypes. USNM 199412. 10.1 mm.

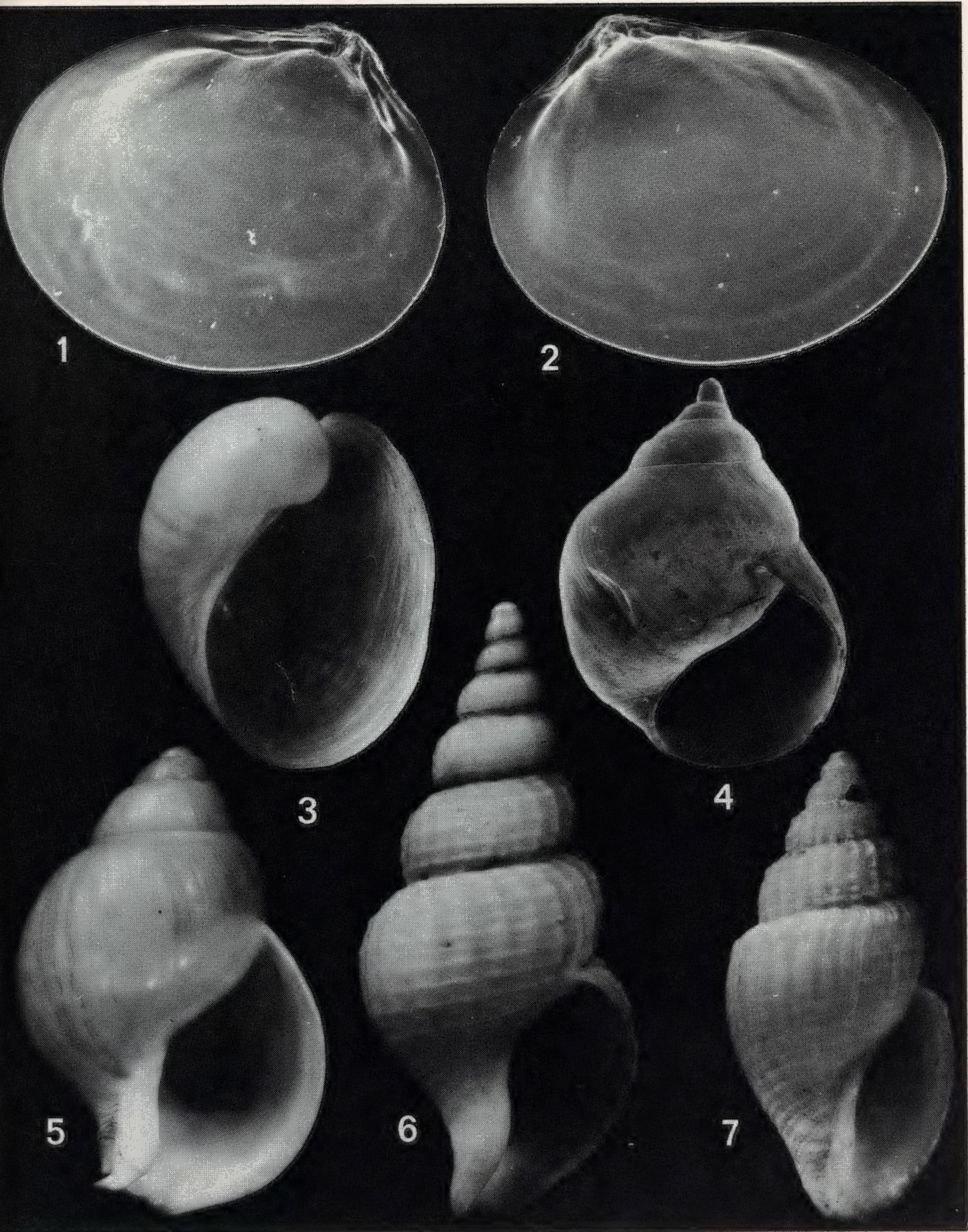
#### PLATE 10.

Figs 1–4. *Sphaenia binghami*, paralectotypes. USNM 171240. 10 mm. Figs 5–8. *Tellina lineata*, syntype. USNM 178267. 10 mm.

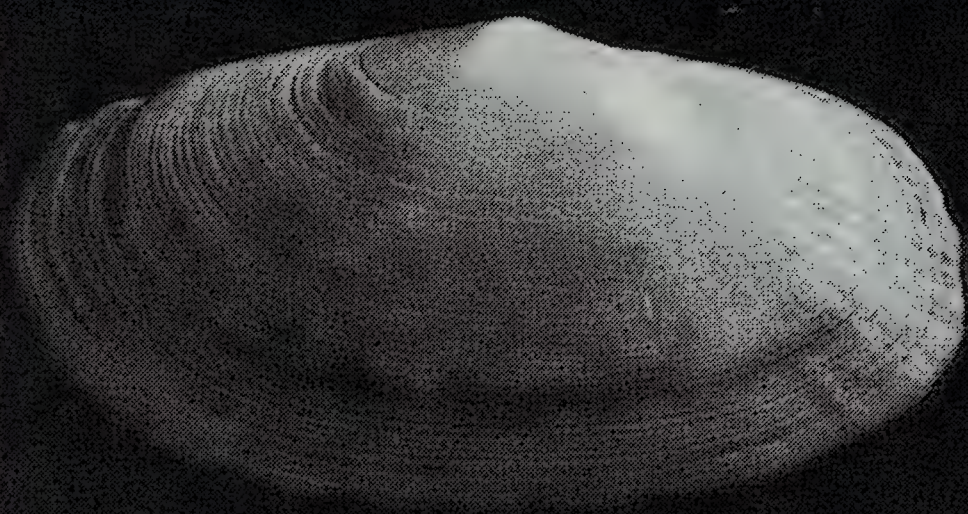
#### PLATE 11.

Title page of Turton's 'Conchological dictionary', with two portraits of the author, placed *vis a vis* against a black background. These portraits were also reproduced in *The Naturalist*, no. 731, Dec. 1917, page 374, in a comment on a talk.

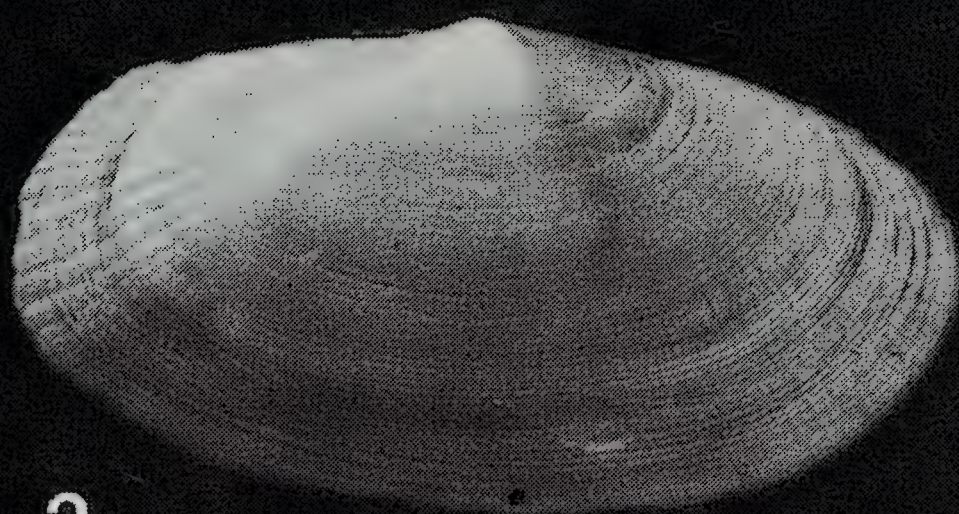




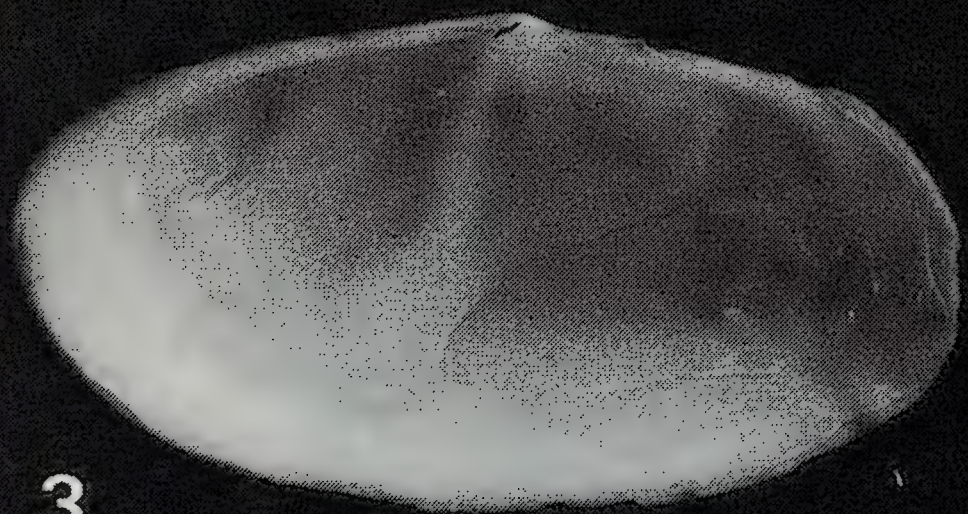




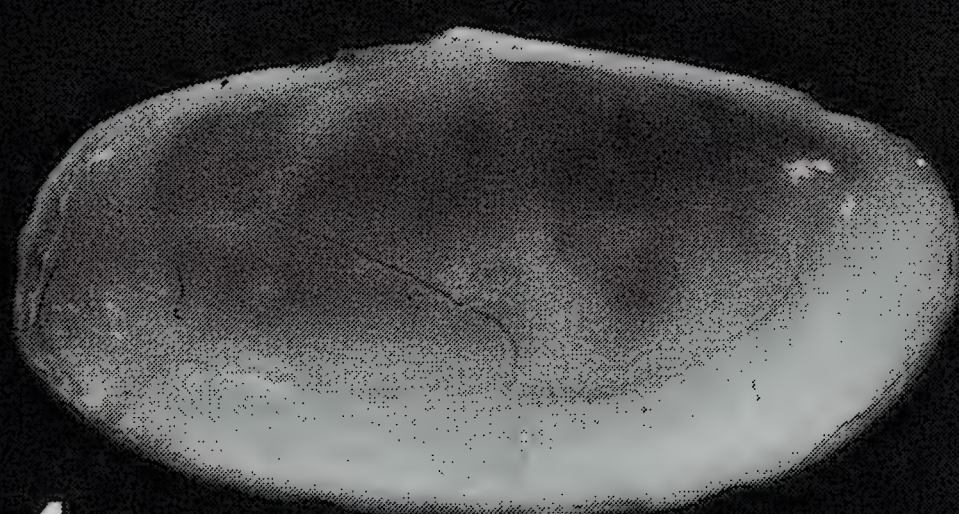
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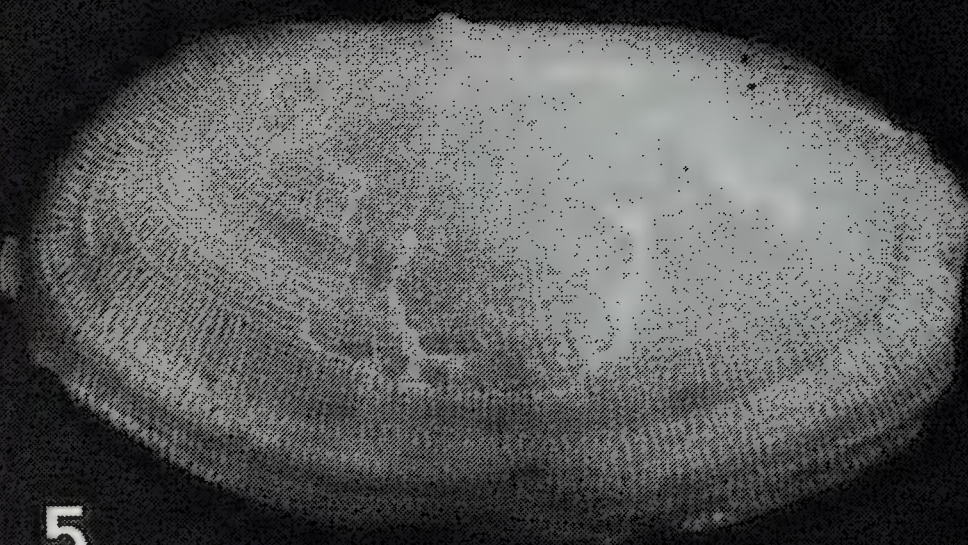
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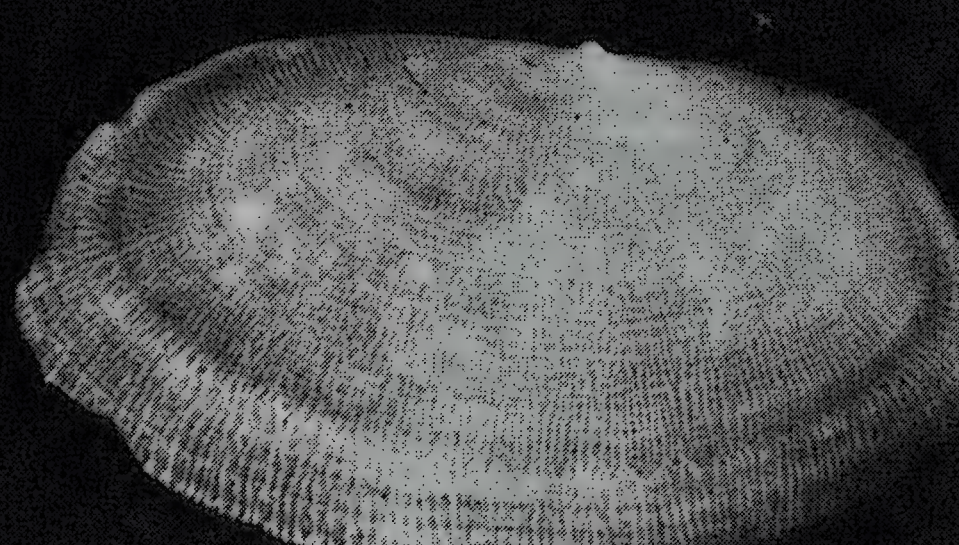
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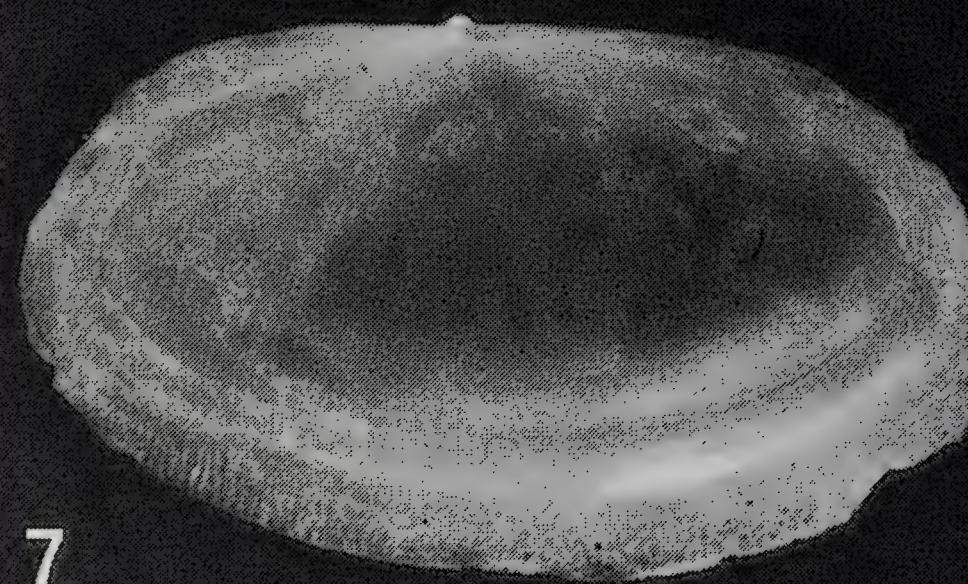
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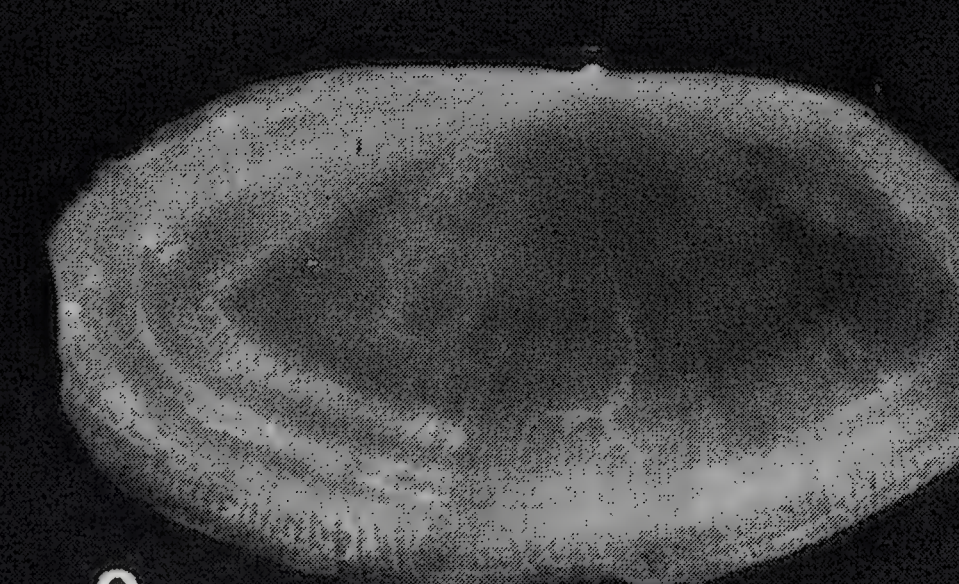
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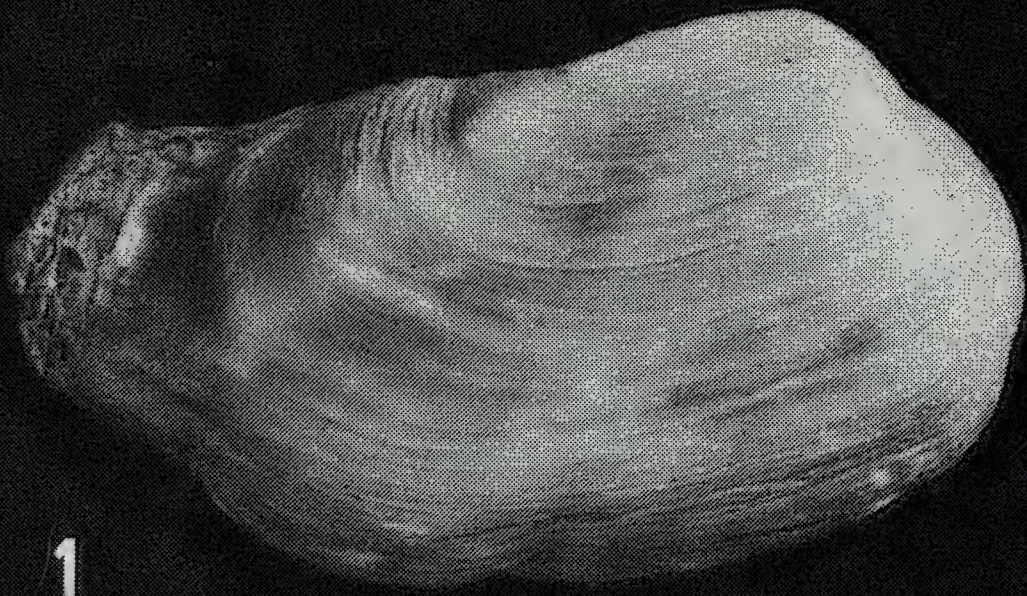


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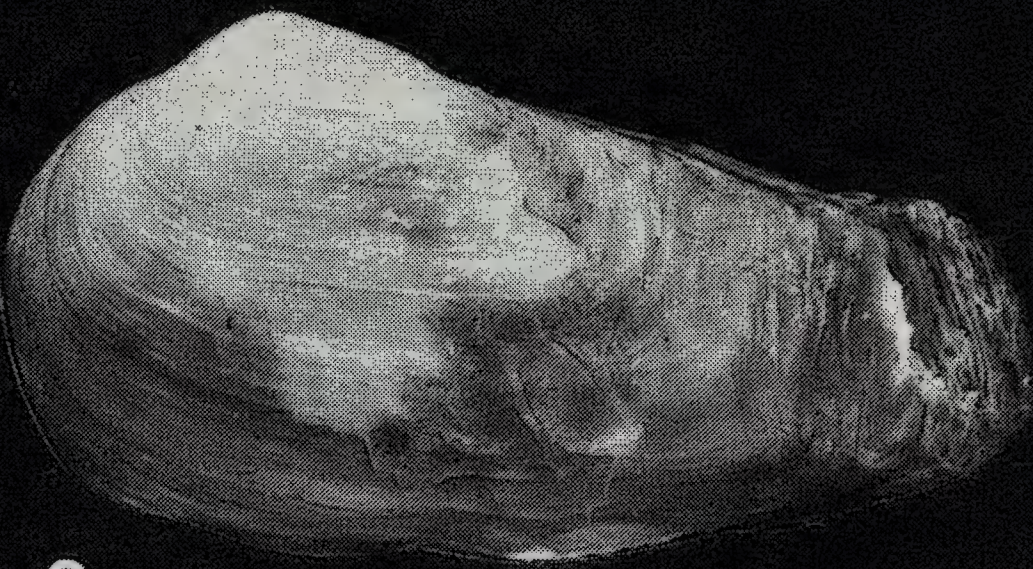


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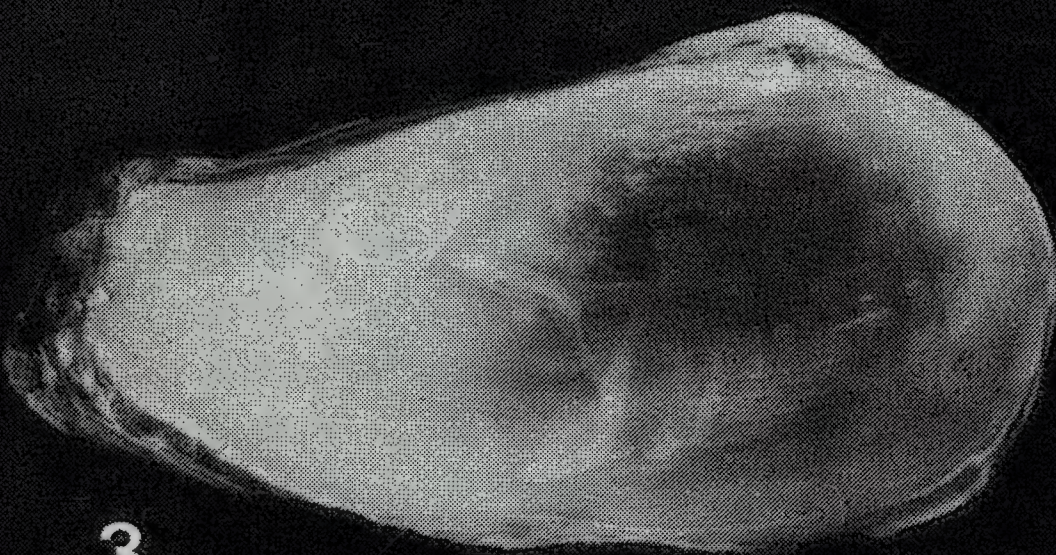




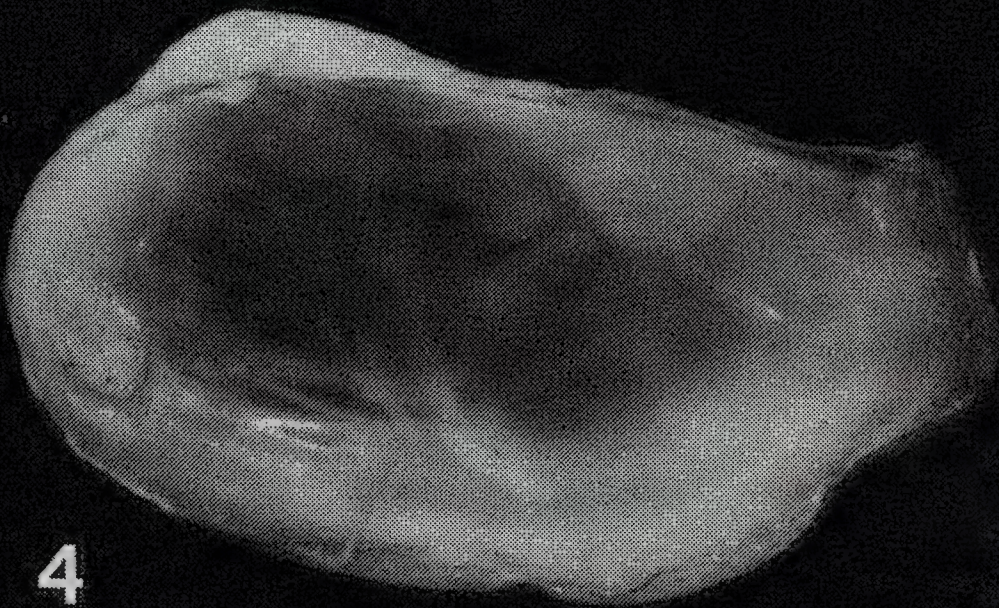
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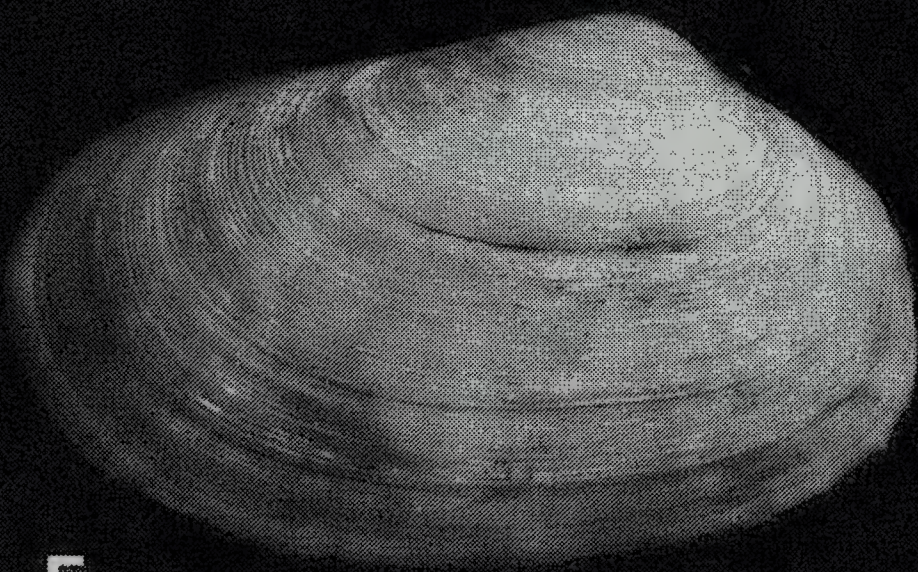
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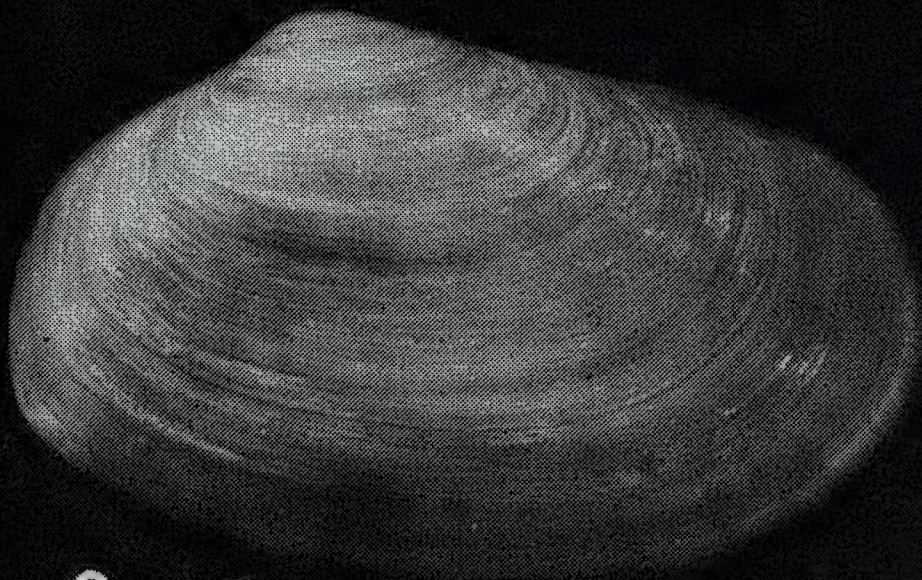
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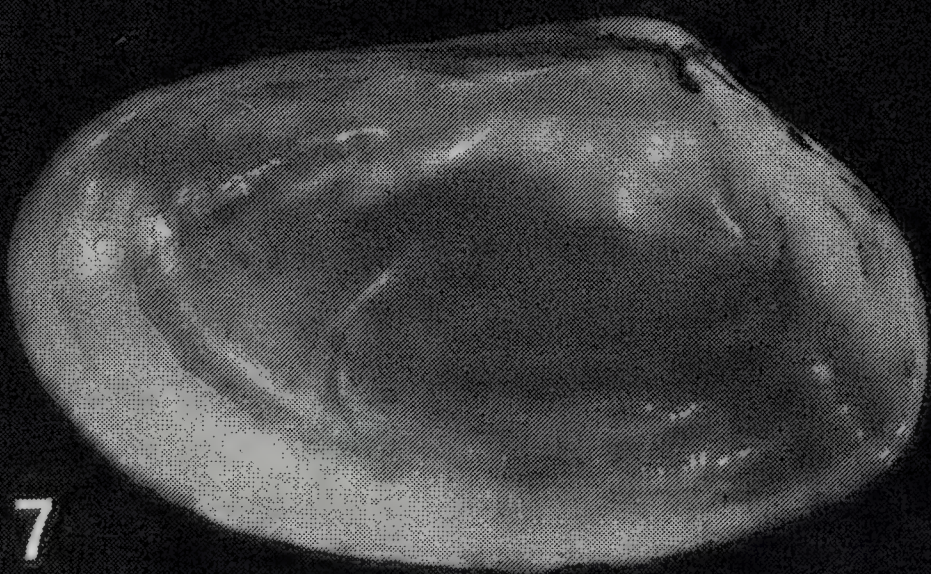
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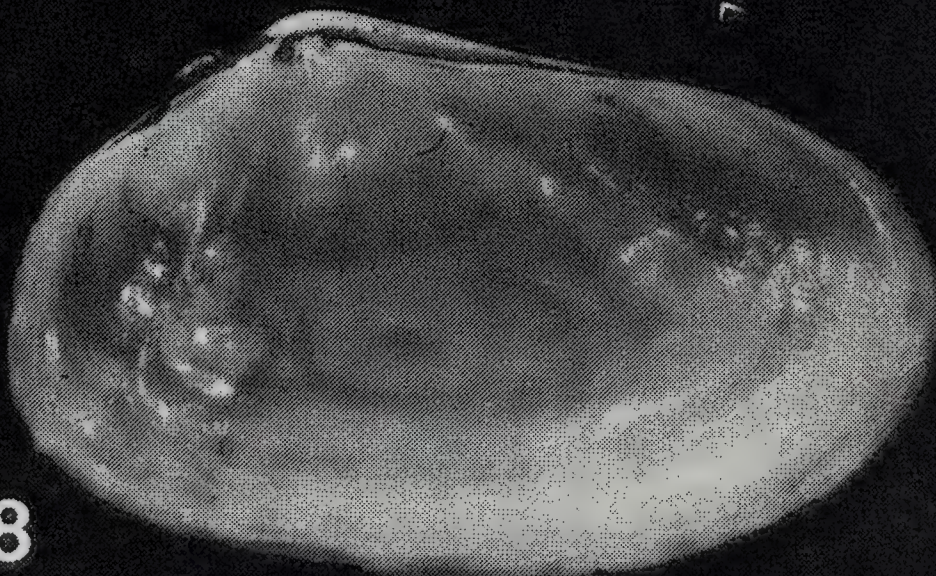
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8



A  
CONCHOLOGICAL  
DICTIONARY  
OF  
The British Islands.  
BY  
WILLIAM TURTON, M.D.  
ASSISTED BY  
HIS DAUGHTER.



"Hæc studia adolescentiam alunt, senectutem oblectant, secundas  
res ornant, adversis solatium et perfugium præbent."

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London :  
PRINTED FOR JOHN BOOTH,  
DUKE STREET, PORTLAND PLACE.

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1819.



- perforans*/*Arca*/Turton 1819, p. 9. Type locality: Teignmouth Harbour (S Great Britain). Type material: Lost. This is *Arca lactea* Linnaeus (Jeffreys 1864, p. 179).
- picta*/*Purpurea*/Turton 1825, p. 365. Type locality: British Channel. Type material: Lost. 'This is a West Indian columbellid' (Jeffreys 1867, p. 358). This may possibly be *Rombinella laevigata* (Linnaeus).
- plana*/*Tellina*/Turton 1802. New name for *Tellina depressa* Gmelin.
- politum*/*Dentalium*/Turton, 1819, p. 38. Type locality: Torbay (S Great Britain). Type material: Five syntypes USNM 174968. This is *Dentalium tarentinum* Lamarck (Jeffreys 1865, p. 196).
- punctata*/*Patella*/Turton 1802. New name for *Patella punctulata* Gmelin.
- puteolus*/*Turbo*/Turton 1819, p. 193. Type locality: Dublin Bay; Between Teignmouth and Dawlish; Devonshire (British Isles), Attached to Fuci. Type material: Lost. This is *Lacuna parva* (Da Costa).
- pyramidalis*/*Murex*/Turton 1816, p. 237. Nomen nudum.
- radiata*/*Patella*/Turton 1802. New name for *Patella jamaicensis* Gmelin. (Not *P. radiata* Born).
- reflexa*/*Voluta*/Turton 1819, p. 251. Type locality: 'Taken in a shrimp net at Exmouth (S Great Britain)'. Type material: Holotype USNM 55370. This is *Phytia myosotis* (Draparnaud) (Jeffreys 1869, p. 109).
- reversa*/*Helix*/Turton 1816, p. 239. Nomen nudum.
- ringens*/*Voluta*/Turton (1816, p. 236, nomen nudum) 1819, p. 250. Type locality: 'Inlets of the sea (of the British Isles) with *Turbo ulvae* and *Voluta denticulata*'. Type material: Two syntypes USNM 55351. This is *Phytia myosotis* (Draparnaud) (Jeffreys 1869, p. 109).
- rotalis*/*Patella*/Turton 1802. New name for *Patella rota* Kanmacher, not Gmelin.
- rotula*/*Patella*/Turton 1807, p. 198. New name for *Patella rota* Kanmacher.
- rubicunda*/*Patella*/Turton 1802. New name for *Patella rubella* Fabricius, not Gmelin.
- rubida*/*Patella*/Turton 1802. New name for *Patella sanguinea* Gmelin.
- rufescens*/*Ostrea*/Turton 1802. New name for *Ostrea rufa* Gmelin.
- rugosa*/*Patella*/Turton 1802. New name for *Patella inaequalis* Gmelin.
- sarniensis*/*Venus*/Turton 1822, p. 153. Type locality: Guernsea (S Great Britain). Type material: Lost. A variety of *Venerupis rhomboideus* (Pennant) (Jeffreys 1864, p. 353).
- saxatilis*/*Ostrea*/Turton 1807, p. 162. Type locality: Swansea (S Great Britain). Type material: Lost. This is *Ostrea edulis* Linnaeus (Winckworth 1946).
- *scopula*/*Psammobia*/Turton 1822, p. 98. Type locality: Dredged near Exmouth (S Great Britain). Type material: Lost. This is *Solecurtus scopula* (Turton).
- semistriatum*/*Dentalium*/Turton 1819, p. 39. Type locality: Dublin Bay (Ireland). Type material: Lost. Jeffreys (1865, p. 198) considers the origin of this species uncertain, so I regard the name as a *nomen dubium*.
- sinuosa*/*Crepidula*/Turton 1825, p. 364. Type locality: On a ship, Scarborough (S Great Britain). Type material: Three syntypes USNM 188033. This is *Crepidula plana* Say (Jeffreys 1865, p. 276).
- striolata*/*Anomia*/Turton 1822, p. 233. Type locality: From roots of Fuci (British Isles). Type material: Five syntypes USNM 196082. This is *Anomia squamula* Linnaeus.
- *stylifera*/*Phasinella*/Turton 1825, p. 367. Type locality: On *Echinus esculentus* (British Isles). Type material: Lectotype USNM 177239, here selected. This is *Pelseneeria stylifera* (Turton). Plate 8, fig. 4.
- subantiquatus*/*Murex*/Turton 1807, p. 174. New name for *Murex antiquus* Donovan.
- sulcata*/*Tellina*/Turton 1816, p. 233. (Not Solander in Brander, 1766) Nomen nudum.
- swainsoni*/*Sphaenia*/Turton 1822, p. 37. Type locality: In rocks, Torbay (S Great Britain). Type material: Lost. This is the young of *Mya truncata* Linnaeus (Jeffreys 1865, p. 70).
- tenera*/*Lima*/Turton 1825, p. 362. Type locality: British Channel. Type material: Lost. Jeffreys (1864, p. 88) considered this a variety of *Lima hians* (Gmelin).



*tenuissima*/*Patella*/Turton 1802. New name for *Patella tenuis* Gmelin.

*traversiana*/*Nerita*/Turton 1816, p. 240. Nomen nudum.

*travisii*/*Crenatula*/Turton 1834, p. 350. Type locality: Scarborough (S Great Britain). Type material: Lost. This is *Isognomon alatus* (Gmelin) (Jeffreys 1864, p. 98), a Caribbean species.

*trevellianum*/*Pleurotoma*/Turton 1834, p. 351. Type locality: Scarborough (S Great Britain). Type material: Lectotype USNM 190860 (here selected) and 5 paralectotypes. This is *Oenopota trevelliiana* (Turton). Plate 8, fig. 7.

*tricornis*/*Patella*/Turton 1819, p. 139. Type locality: From *Serpula tubularia*, Portmarnock, near Dublin (Ireland). Type material: Lost. This is the operculum of the annelid *Pomatoceros triqueter*.

*tuberculata*/*Pholas*/Turton 1822, p. 5. Type locality: Exmouth and Torbay (S Great Britain). Type material: Holotype USNM 199946. This is *Barnea parva* (Pennant).

*tuberculatum*/*Buccinum*/Turton 1819, p. 16. Type locality: Exmouth (S Great Britain). Type material: Lost. This is *Nassarius pygmaeus* (Lamarck) (Jeffreys 1867, p. 355).

*tubularis*/*Anomia*/Turton 1822, p. 234. Type locality: Attached to Fuci (British Isles). Type material: Holotype USNM 186087. This is *Anomia squamula* (Linnaeus).

*tumida*/*Ostrea*/Turton 1819, p. 132. Type locality: Among serpulae, Torbay (S Great Britain). Type material: Holotype USNM 196719. This is *Similipecten similis* (Laskey) (Jeffreys 1864, p. 72).

● *turtoni*/*Galeomma*/Turton 1825, p. 361. Type locality: British. Type material: Holotype USNM 199412. Plate 9, figs 5–8.

● *turtonis*/*Turbo*/Turton (1816, p. 238, nomen nudum) 1819, p. 208. Type locality: Many places in Ireland; Balbriggan; Devonshire (S Great Britain). Type material: Lost. This is *Epitonium turtonis* (Turton).

*varicosa*/*Tritonia*/Turton 1825, p. 365. Type locality: Torbay (S Great Britain). Type material: Lost. This is *Nassarius pygmaeus* (Lamarck) (Jeffreys 1867, p. 355).

*velutinus*/*Mytilus*/Turton 1816, p. 235. Nomen nudum.

*vermigera*/*Doris*/Turton 1807, p. 134. Type locality: Swansea (S Great Britain). Type material: Lost. This is *Aeolidia papillosa* Linnaeus fide Winckworth (1946).

*zonata*/*Bulla*/Turton 1834, p. 352. Type locality: Lands End (S Great Britain) Type material: Lost. This is the young of *Scaphander lignarius* (Linnaeus) (Jeffreys 1867, p. 445).

#### ACKNOWLEDGEMENTS

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## REVIEW

*Invertebrates of the Wadden Sea. Report 4.* By N. K. H. Dankers and W. J. Wolff, 1981. Published and distributed by A. A. Balkema, P.O. Box 1675, Rotterdam, Netherlands. Hfl. 24, 50.

This report is one of a series of eleven reports on the Wadden Sea covering Geomorphology; Hydrography; Flora and Vegetation; Invertebrates; Fishes and Fisheries; Birds; Mammals; Pollution; Flora and Vegetation of the Islands; Fauna of the islands; Physical planning and nature management in the area.

The Wadden Sea described as "Europe's largest marine wetland" is situated along the western and northern coasts of Denmark, the Federal Republic of Germany, and the Netherlands. It is a shallow coastal sea bounded on its outer edge by 17 large inhabited barrier islands as well as small uninhabited islands and sand-banks.

Report 4 covers the invertebrates, and is made up of a large number of individual scientific papers submitted to, and by, the "Marine Zoology" section of the Wadden Sea Working Group. For the purpose of the report the papers are divided into 10 main sections as follows:—

- 1 Conclusions and Recommendations;
- 2 Invertebrates of the Wadden Sea; An Introduction;
- 3 The species of invertebrates occurring in the Wadden Sea;
- 4 Relationships between species and their environment;
- 5 Life histories of some important Wadden Sea invertebrates;
- 6 Quantitative data on the Plankton of the Wadden Sea proper;
- 7 Quantitative data on the Benthos of the Wadden Sea proper;
- 8 The Invertebrates of the estuaries of the rivers;
- 9 Microfauna of the Wadden Sea;
- 10 The role of the larger invertebrates in the Wadden Sea ecosystem.

The Molluscan fauna of the Wadden Sea is examined from several different aspects, and a full list of species is given under section 4, in which 89 species are mentioned: 2 Amphineura; 47 gastropoda, (including 29 sea-slugs), 35 lamellibranchia and 4 cephalopoda. Life histories, populations and annual yields are discussed in section 5 on the four most important marine bivalves; *Mytilus edulis*; *Cerastoderma edule*; *Macoma balthica* and *Mya arenaria*.

The most important contribution of this publication, however, is the detailed information about the inter-relationships of species within the environment as shown by completely independent and differing research techniques.

All eleven reports can be acquired from the publishers, bound in a set of three, entitled "Ecology of the Wadden Sea". Individual papers within the reports can be easily criticised, but together as a whole unit the report is well worth perusal, particularly because of the area's proximity to marine environments of the United Kingdom.

A. NORRIS



# A BRIEF REVIEW OF THE SPECIES OF *GONAXIS* TAYLOR SUBG. *PSEUDOGONAXIS* THIELE (*PULMONATA: STREPTAXIDAE*)

BERNARD VERDCOURT\*

(Accepted for publication, 16 October 1982)

*Abstract:* *Gonaxis* subg. *Pseudogonaxis* Thiele is revised, 7 species being recognised.

## INTRODUCTION

This very distinct group with strongly distorted markedly striate rather small shells was first proposed by Thiele (1932) (1934 p. 1010) as a subgenus of *Tayloria* Bgt. Despite the characteristic appearance, I have preferred to maintain it as a subgenus of *Gonaxis* rather than as a genus until the complete anatomy of many more *Gonaxis* (sensu lato) species is known. I have already given some account of the anatomy of *G. (P.) percivali* (Preston) (Verdcourt 1961) but none of the other species appears to have been so examined. The following recent species-group taxa belong to this subgenus, listed in chronological order: *kirkii* Dohrn 1865, *pusillus* von Martens 1897, *nsendweensis* Putzeys 1899 (type of subgenus), *cavallii* Pollonera 1906, *percivali* Preston 1913, *woodhousei* Preston 1913, *cavallii ituriensis* Pilsbry 1919 and *stenostoma* Verdcourt 1965. A species, *protocavallii* Verdcourt 1963, which is clearly closely allied to *G. pusillus*, is also known from the Miocene of Kenya, demonstrating that the subgenus has scarcely changed at all in some 20 million years, at least in shell shape. The distribution of the subgenus is unusual since it apparently does not occur on any of the newer mountains, Kenya, Kilimanjaro, Meru nor on the Aberdares, nor on the very new Nyambeni Hills with (at least formerly) mollusc-rich forests, nor in the Crater Highlands of Tanzania. It is also absent from the much more ancient elevated areas of the Usambaras, Ulugurus and Southern Highlands in Tanzania. Outside of East Africa it is known from Malawi, Mozambique, E. Zaire and S. Sudan. Unless the species have been extensively overlooked by collectors, which seems a little unlikely since they are by no means minute, I am at a loss to explain this restricted area of distribution. Unfortunately the actual ecology of most of the species is not fully known. The outlying station Malka Mari is presumably an area of riverine woodland along the Daua Parma in an otherwise arid area. Marsabit Mt. is covered with evergreen forest of a rather dry type maintained by mist rather than rainfall; the Naivasha locality is vague but I have assumed that some rather dry wooded locality near the lake and town is indicated rather than a wetter area to the east on the flanks of the Aberdares. The single certain Tanzanian record is from a tree-termite's nest, clearly in rather dry woodland. On the other hand the Elgon, Entebbe, Ruwenzori and Ituri Forest localities are certainly from wetter forested areas; the Ruwenzori sites are at 1800–2000 m. in the Butagu and Mobuku Valleys in lower montane forest; the Ituri Forest sites at Penge, Avakubi, Semliki Forest at Lesse, the gallery forest of the Rutshuru R. and Bwamba Valley are undoubtedly areas of dense rain forest.

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## KEY TO THE SPECIES

1. Apical  $2\frac{1}{2}$  whorls smooth; shell very distorted,  $11 \times 7$  mm; aperture relatively narrower,  $5.5 \times 3.8$  mm (extreme N.E. Kenya) *G. stenostoma*  
Only initial  $\frac{1}{2}$ –1 whorl smooth; shell much less to almost as distorted; aperture relatively wider 2
2. Shell relatively less distorted, the apical whorls forming a more obvious subacute spire so that when shell is lying on a flat surface with aperture uppermost the apical whorls are visible;  $10$ – $11.5 \times 7.5$ – $8.5$  mm; aperture  $5$ – $5.5$  mm wide; umbilicus relatively narrower (N. Kenya) *G. percivali*  
Shell relatively more distorted the apical whorls forming a spire which is not evident when shell orientated as above; spire usually much flatter but more elevated in *G. kirkii* 3
3. Spire raised, more or less containing an angle of  $90^\circ$ ; shell  $8$ – $8.8 \times 5.5$ – $6.4$  mm; striae obsolescent on whorl above aperture (Malawi & Mozambique) *G. kirkii*  
Spire flatter containing a larger angle 4
4. Shell larger,  $10.5$ – $12.3 \times 8.5$ – $9.5$  mm, relatively slightly broader, the ratio  $1.23$ – $1.3$ ; costae around umbilicus and above aperture very crisply marked; umbilicus relatively wider (E. Zaire) *G. nsendweensis*  
Shell small,  $7.6$ – $11$  (– $12$ )  $\times 5.5$ – $8.2$  mm, relatively slightly narrower, the ratio  $1.36$ – $1.41$ ; costae around umbilicus and above aperture either crisply marked or more obscure 5
5. Shell very distorted, when held sideways the penultimate whorl very distinctly projecting beyond the lateral profile of the spire 6  
Shell less distorted, when held sideways with penultimate whorl scarcely projecting beyond the lateral profile of the spire 7
6. Penultimate whorl very strongly keeled *G. sp. nov.*  
Penultimate whorl not keeled; differs from *pusillus* also in upper of two whorls visible when shell lying with aperture uppermost, appearing the broader; striae around umbilicus and above aperture very strong and spiral striae between them quite marked; aperture more narrowed towards the apex; shell  $9.8$ – $11 \times 6.4$ – $7.5$  mm; Ruwenzori at about 2000 m. *G. cavallii*
7. Costae around the umbilicus and above the aperture clear and distinct; shell  $7.6$ – $9.5 \times 5.5$ – $7$  mm *G. pusillus pusillus*  
Costae around the umbilicus and above the aperture usually much more obscure; shell  $9$ – $11$  (– $12$ )  $\times 6.3$ – $8.2$  mm *G. pusillus woodhousei*

SPECIES<sup>1</sup>*Gonaxis percivali* (Preston 1913)1913 *Streptaxis percivali* Preston, p. 194, pl. 32, fig. 41960 *Gonaxis percivali* Verdcourt, p. 258 (pro parte)1961 *Gonaxis percivali* Verdcourt, p. 15, 20 fig. 11 (pro parte)

KENYA. N. Slopes of Marsabit Mt., forest, Percival (holotype in MRAC 16939; paratypes at BM 1912.9.19.46–47); S. Marsabit, J. G. Williams (Nat. Museum, Nairobi); B. Verdcourt, Aug. 1957, (Nat. Museum, Nairobi; MRAC 792099). N. Slopes of Mt. Nyiro, S of Sake on L. Rudolf (now L. Turkana) (BM).

<sup>1</sup>The following abbreviations are used for Museums:— AMNH—American Museum of Natural History, New York. BM—British Museum (Natural History). ANSP—Academy of Natural Sciences, Philadelphia. MRAC—Musée Royal de l'Afrique Centrale, Tervuren. SMF—Senckenbergische Museum, Frankfurt am Main.



*Gonaxis kirkii* (Dohrn 1865)

- 1865 *Streptaxis kirkii* Dohrn, p. 232  
 1905 *Streptaxis (Gonaxis) kirkii* Kobelt, p. 8, pl. 42, figs. 14, 15  
 1920 *Streptaxis kirki* Germain, p. 27  
 1925 *Gonaxis kirki* Connolly, p. 110  
 1939 *Gonaxis kirki* Connolly, p. 13

MOZAMBIQUE. Maputo District [Lourenço Marques]; Mtisherra R. Valley, Cressy (BM); Chimoio District (not found).

MALAWI. Lake Malawi, Mumba I., J. Kirk (syntype BM 62.9.25.20).

Germain suggested that *woodhousei* and *percivali* were conspecific with this and it is possible he will ultimately prove to be correct but until more material is available and all the taxa have been dissected I have maintained them separate; if *kirkii* does prove merely another subspecies of this complex then it will be the epithet which has to be used for the species as a whole, being much older than *pusillus*. In size and lack of sculpture above the aperture it resembles *pusillus woodhousei* but in its more produced spire it is close to *percivali*. The paratype of *kirkii* preserved at the British Museum is unfortunately worn and no other material has been collected in Malawi as far as is known.

*Gonaxis pusillus pusillus* (von Martens 1897)

- 1897 *Streptaxis pusillus* von Martens, p. 32, pl. 2, fig. 31  
 1919 *Gonaxis pusillus* Pilsbry, p. 180  
 1919 *Gonaxis cavallii ituriensis* Pilsbry, p. 177, fig. 63c

By comparison of a series of paratypes of Pilsbry's race *ituriensis* lent to me by Musée Royal de l'Afrique Centrale with the syntypes of Von Marten's species very kindly loaned from Berlin by Dr. R. Kiliass the above synonymy is established without doubt. Although the majority of the paratypes of *cavallii ituriensis* are larger than the types of *pusillus* several differ only by fractions of a mm; the sculpture is also identical in every way. Pilsbry had been misled when he stated '*G. pusillus* . . . is a smaller shell, of much less oblique shape, according to v. Martens' figures'; unfortunately von Martens' figure is not accurate and was probably prepared from the one of the three syntypes which is I believe rather abnormal. Also von Martens' method of measuring the distorted shell differed from Pilsbry's. J. Bequaert (in Pilsbry 1919, p. 180) has already shrewdly suggested the synonymy and his remarks are worth repeating. Dealing with the type locality of *pusillus* he writes 'Type locality: "Bukendo am Ituri Fluss" (Stuhlmann Coll.).' I believe that by this is meant Bukende in the Semliki Valley, 'Ituri' being then a misspelling for 'Itiri'. No locality 'Bukendo' is mentioned near the Ituri River by Stuhlmann in the report of his journey. If my supposition be true, *G. pusillus* was found very close to Lesse, where I collected numerous *G. cavallii ituriensis* and it becomes a question whether the latter is not after all a synonym of *G. pusillus*.

ZAIRE. Ituri Forest: Penge, Bequaert (AMNH holotype of *cavallii ituriensis*, paratypes in MRAC 16673-16721 and presumably ANSP); Avakubi, Bequaert (probably ANSP); Alasinda?, 3 May 1925 Schouteden (MRAC 554450) (worn and deformed shell); Semliki Forest: Lesse, Bequaert (probably ANSP); Bukende, Stuhlmann (syntypes of *pusillus* in Zoological Museum, East Berlin). Rutshuru, gallery forest of the Rutshuru River. Bequaert (ANSP).

UGANDA. Kidama, Pitman (BM). Entebbe, G. D. Hale Carpenter (BM, National Museum, Nairobi); Entebbe, ex Fulton (MRAC 16585). Mabira Forest, R. L. Harger (BM).

*Gonaxis pusillus woodhousei* (Preston 1913)

- 1913 *Streptaxis woodhousei* Preston, p. 194, pl. 32, fig. 5  
 1923 *Gonaxis woodhousei* Germain, p. 12 pl. 1, figs. 6, 11



- 1923 *Gonaxis percivali* Germain, p. 11, pl. 1, figs. 1–3, 7 (pro parte)  
 1927 *Gonaxis woodhousei* Connolly, p. 170  
 1960 *Gonaxis percivali* Verdcourt, p. 258 (pro parte)  
 1961 *Gonaxis percivali* Verdcourt, p. 20 (pro parte)

SUDAN. Didinga District, Nagichot, Hale Carpenter (BM).

UGANDA. N. foot of Ruwenzori, Bwamba Pass and Valley, Hale Carpenter (BM; National Museum, Nairobi). Mt. Elgon, Woodhouse (holotype MRAC 16586; ?paratype MRAC 16587 ex Preston; paratype Liverpool Museum ex Salisbury collection; ? paratypes BM ex Kennard collection; paratypes BM 1912.8.18.41–3 & 1937–12–30.109–113); Mt. Elgon, Woodhouse (stages of growth, possibly paratypes BM); Mt. Elgon (BM ex Biggs collection); Mt. Elgon, no collector, Salisbury collection 1965.141 (Liverpool Museum). W. Ankole, R. Kagera, Bugoma Forest, Pitman (BM). Bunyoro, E. Lake Albert, Kyangwali, Pitman (BM). No locality, Percival—F 322 (National Museum Nairobi—possibly three wrongly labelled paratypes of *woodhousei* which they exactly match—not *percivali*); no locality, ex W. F. Webb, MRAC 612547–8 (labelled *perturbata* Preston, an MS name).

KENYA. Naivasha, Hale Carpenter (BM, National Museum, Nairobi).

TANZANIA. Mahari Peninsula, near Kasoge, in termites' nest, 780 m., 29 July 1959, Eccles 132 (2nd Oxford Univ. T.T. Expedition) (National Museum, Nairobi).

This has never been refound at Naivasha despite the locality being well-known and the record needs confirmation. This Kenya material differs slightly from typical *woodhousei* in a number of ways and the striation is almost that of *pusillus pusillus*.

The Bwamba material is somewhat worn; by rights it ought to belong to race *pusillus*, the Ituri race, but the shells are up to 11×8.3 mm and the situation not so clear.

*Gonaxis cavallii* (Pollonera 1906)

- 1906 *Streptaxis cavallii* Pollonera, p. 2  
 1909 *Streptaxis cavallii* Pollonera, p. 183, pl. 20, fig. 1  
 1919 *Gonaxis cavallii* Pilsbry, p. 176, figs. 63b, b<sup>1</sup>

ZAIRE. Ruwenzori Mts., western slopes, Butagu Valley, 1800–2000 m., Bequaert (ANSP; MRAC 16611)

UGANDA. Ruwenzori Mts., eastern slopes, Mobuku Valley, about 2000 m., Abruzzi Exped. (holotype in Zoological Museum, Turin).

I have maintained *cavallii* as a species and some specimens from lower altitudes which I formerly associated with the name I now prefer to look on as large *G. pusillus woodhousei*.

Unfortunately, although obviously common according to Bequaert, no material was collected in spirit at that time, nor since, although it must still be common in such a relatively undisturbed area.

*Gonaxis nsendweensis* (Putzeys 1899)

- 1899 *Streptaxis nsendweensis* Putzeys, p. lv, fig. 3 (u clearly a misprint)  
 1900 *Streptaxis nsendweensis* Dupuis & Putzeys, p. xix  
 1919 *Gonaxis nsendweensis* Pilsbry, p. 179, figs. 63a & a<sup>1</sup>  
 1960 *Tayloria (Pseudogonaxis) nsendweensis* Zilch, p. 557–8, fig. 1949  
 1961 *Tayloria (Pseudogonaxis) nsendweensis* Zilch, p. 80

ZAIRE. Nsendwe, Dupuis (holotype and paratypes MRAC 16797–16831; paratypes in BM 1901.4.25.1–2, 1901.8.1.37–9 and 1937.12.30.71–4 and also one lot ex Macandrew collection; ANSP; National Museum, Nairobi and Zoological Museum, East Berlin)



VERDCOURT: *GONAXIS* SUBG. *PSEUDOGONAXIS*

*Gonaxis stenostoma* Verdcourt 1965

1960 *Gonaxis percivali* Verdcourt, p. 258 (pro parte)

1965 *Gonaxis stenostoma* Verdcourt, p. 165, fig. 2

KENYA. Northern Frontier Province: Malka Mari [Melka Murri], J. G. Williams (holotype in SMF 181612)

Only one specimen has been seen but the locality is a remote one only rarely visited.

*Gonaxis* sp. nov.

Two worn specimens from Zaire seem to represent an extraordinary new species. The penultimate wall not only projects very strongly from the lateral profile of the shell but is very strongly keeled, the keel itself very narrowly rounded and strongly compressed above and beneath. The fact that there are two exactly similar specimens seems to indicate it is almost certainly not a chance abnormality of some more conventionally shaped member of the section. The material is not really adequate for description.

ZAIRE. About 100 km E. of Kisangani [=Stanleyville], Bafwasende District, R. Tshopo, Bafwaboli, 480 m., Raemakers (MRAC 624011-2)

*Gonaxis* sp.

TANZANIA. Langenburg [=Tukuyu], Fülleborn; Russayo, Hösemann (Zoological Museum, East Berlin).

When I examined this material in 1959, I suggested it could be the young of *G. nsendweensis* but this seems unlikely. Adult material is needed from the area. I have not re-examined the material.

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PLATE 12.

- Species of *Gonaxis* subg. *Pseudogonaxis*. Figs. 1-3. *G. percivali*, Kenya, Marsabit, B. Verdcourt MRAC 792099.
- Figs. 4-6. *G. pusillus pusillus*—paratype of *G. cavallii ituriensis* MRAC 16673.
- Figs. 7-9. *G. pusillus pusillus*, Uganda, Entebbe, MRAC 16585.
- Figs. 11-12. *G. pusillus woodhousei*—probable paratype MRAC 16587.

PLATE 13

- Species of *Gonaxis* subg. *Pseudogonaxis*. Figs. 1-3. *G. cavallii*, Zaire, Ruwenzori, Bequaert MRAC 16611.
- Figs. 4-6, 7-9. *G. nsendweensis*, Zaire, Nsendwe, two paratypes MRAC 16797 a and b.
- Figs. 10-12. *G. sp.*, Zaire, Bafwaboli, Raemakers MRAC 624011.
- Figs. 13, 14. *G. stenostoma*, Kenya, Malka Mari, J. G. Williams holotype SMF 181612. All×3.



# THE IDENTITY OF *HELIX BUTUMBIANA* VON MARTENS (*PULMONATA: ENDODONTIDAE* *SENSU LATO*)

BERNARD VERDCOURT\*

(Accepted for publication, 16 October 1982)

*Abstract:* *Helix butumbiana* von Martens is shown to be identical with the small snail later described by Germain as *Prositala fernandopoensis*. It is easily recognised by its remarkable sculpture. Study of the radula shows that Thiele was correct in referring it to the Endodontidae *sensu lato* but a more precise placing must await dissection of fresh material.

## INTRODUCTION

In 1959 I visited the Zoological Museum in East Berlin to work through the rich collections of African snails described by Jickeli, E. von Martens and J. Thiele. I examined the holotype of *Helix butumbiana* von Martens (1895) and it was clear that it was not a member of the Helicidae as indeed was suggested from the figure given by von Martens (1897) in a later work. Germain (1913), who almost certainly had never examined the original material, made this species the basis of *Halolimnohelix* subg. *Massaihelix*, the name being based on the very mistaken belief that the type locality Migere in Butumbi, Uganda was in Masai country whereas the nearest Masai are some 350 miles to the east! Again without any evidence Pfeffer (1931) raised *Massaihelix* to generic rank and suggested it might be synonymous with *Percivalia* Preston, actually a much larger Urocyclid! Unfortunately the holotype of *Helix butumbiana* has the sculpture worn away but I (1969) suggested it might belong near *Sitala iredalei* (Preston) and its relatives (now placed in the genus *Afroconulus* recently described by van Mol and van Bruggen (1971)) or to *Trachycystis* subg. *Psichion*; I also pointed out that it resembled *Prositala fernandopoensis* Germain but had a lower wider shell. There the matter rested until two circumstances again drew it to my attention. Working through the large collection of East African snails made during a period of over 35 years by Åke Holm, sent to me on loan from the Natural History Museum, Stockholm, a few small shells with very characteristic sculpture jogged my memory; and secondly, mixed with African streptaxids at the British Museum (Natural History) I discovered a paratype of *Helix butumbiana* with the sculpture better preserved than on the Berlin holotype. It is possible that the latter was damaged by Thiele who is known to have virtually destroyed many types by boiling in sodium hydroxide to extract radulae in the desperate hope of establishing the taxonomic positions of the species involved. The extraordinary sculpture immediately reminded me that that of Germain's *Prositala fernandopoensis* was very similar. There was no doubt that the Holm material was identical with *Helix butumbiana* and during a visit to the Laboratoire de Malacologie, Paris in March 1982 I was able, through the kindness of Dr. S. Tillier, to compare the Holm specimens with the series of syntypes and other material of *Prositala fernandopoensis* and it is clear they are conspecific. Many of the specimens from Fernando Po (now Malabo) are taller but there is a good deal of variation and some specimens are an identical match; moreover, there are no long series from East Africa to make a proper comparison. The synonymy may be set out as follows.

\*Spring Cottage, Kimbers Lane, Maidenhead, Berks.



**Prositala butumbiana** (von Martens 1895)

- 1895 *Helix butumbiana* von Martens, p. 179  
1897 *Helix butumbiana* von Martens, p. 58, t3, fig. 22  
1915 *Sitala* (*Prositala*) *fernandopoensis* Germain, p. 288  
1916 *Sitala* (*Prositala*) *fernandopoensis* Germain, p. 231, pl. 9, fig. 11 & pl. 10, figs 9–11  
1928 *Sitala* (*Prositala*) *fernandopoensis* Connolly, p. 538  
1969 *Helix butumbiana* Verdcourt, p. 176, 180

DISTRIBUTION

MALABO (Fernando Po): Bahia de S. Carlos, Basile, 200–400 m., Dec. 1901, leg. L. Fea (Paris and Genoa, syntypes); leg. L. Fea, no other data (Paris labelled 'cotypes'); Basile, 400–600 m., leg. L. Fea (Paris and Genoa—2 tubes) (4 lots in all, presumably collected about the same time\*)

SIERRA LEONE: Panguma, leg. Blacklock (BM)

CAMEROON: Bitze, leg. Bates (BM)

UGANDA: Kigezi District, Butumbi, Migere, *Stuhlmann* (holotype of *Helix butumbiana*, Berlin; paratype, BM 1893. 3.22.13). Toro District, leg. Fisher (BM) (not found)

KENYA: Kakamega Forest, Kisieni, 1600 m., 19–21/1. 1969, leg. Å. Holm 138 & 141 (Stockholm). Cherangani Hills, Kamatira Forest, 2270 m., 23.1.1965, leg. Å. Holm (Stockholm)

In order to aid recognition I give an outline drawing of the shell (Fig. 1) and details of the sculpture as revealed by a Scanning Electron Microscope (Plate 14). The shell is 'euconuloid' in shape and measures about  $4.5 \times 4 \times 3.5$  mm, with  $6\frac{1}{2}$  whorls; the sculpture consists of excessively close interrupted spiral striae 10 being contained in 0.11–0.13 mm. The umbilicus is narrow and the columella reflected over it. The natural colour of the shell is greyish white and the sculpture gives it a resemblance to finely cut glass.

The distribution given above clearly cannot be complete. It must occur in many intermediate stations; however, it is well known that the fauna and flora of parts of western Kenya and Uganda have strong affinities with those of W. Africa. The few known stations are indicated on a map (Fig. 2) and they fit in very well with dispersal pathways which would have existed at a pluvial maximum when continuous highland forest stretched from Guinea to west of L. Victoria. Where the species originated and in which direction the spread occurred is conjectural but the present distribution suggests a W. African origin. A small mollusc travels at about 0.3 mm. per second giving a surprising minimum necessary time for a spread from a Cameroun centre of only 370 years but since populations would have been stationary much of the time and moving at random for other periods the time needed might well be more in the order of tens or even hundreds of thousands of years. There have been marked climatic changes in Africa during the past 50,000 years and the present balance of forest (i.e. as it was before man destroyed most of it) is the result of changes as recent as 8,000–16,000 years ago. Up until that time a 100 m. lowering of the sea level put Fernando Po in contact with the mainland. The Cameroun pathway being little over 500 m. has only been forested with montane forest at times corresponding to severe glaciations elsewhere. The lack of even subspecific differences between Camerouns populations and East African populations of some plants and animals suggests some migrations have been quite recent.

\* Some of this material also bears the name R. Gestro; he was not the collector but Director of the Genoa Museum at the time in 1914 when the material was sent to Paris.



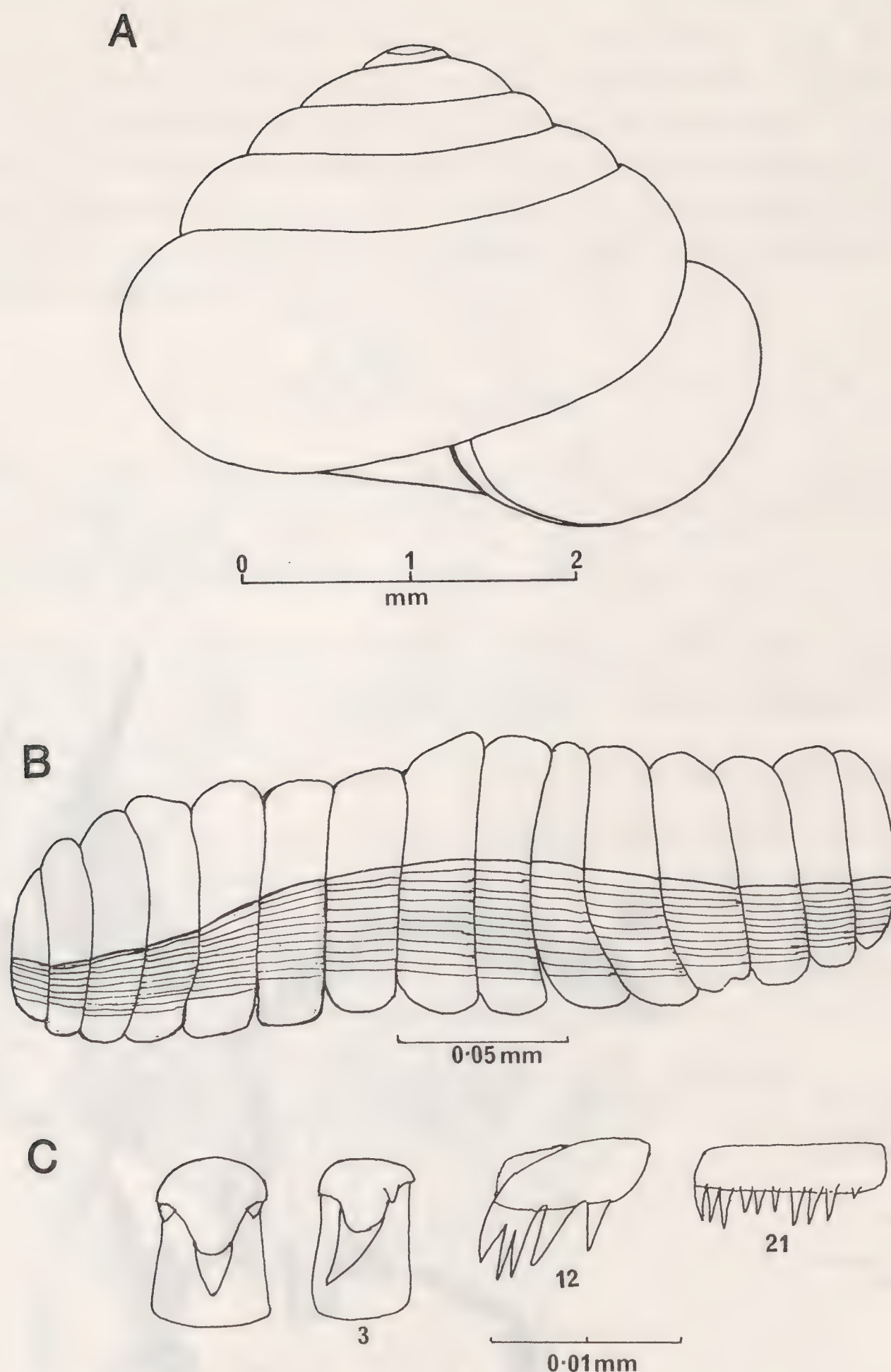


Fig. 1. *Prositala butumbiana* (von Martens). A shell of syntype; B jaw of syntype; C selected teeth from radula of syntype.

Not enough is known of the ecology of *Prositala* to comment further but although clearly in montane forest on the Cherangani Hills and probably in Toro, elsewhere it is in lowland forest and seemingly adaptable. Only 14 East African species show this East-West distribution e.g. *Gulella avakubiensis* Pilsbry, *G. conospira* (von Martens), *G. pupa* (Thiele), *G. tudes* (von Martens), *Trochozonites adansoniae* (Morelet) and *T. bifilaris* (Dohrn). It is probable that the pathways were not open all the way for any one long period of time and that migrations of organisms not capable of flight or rapid motion probably happened in stages; only a restricted number of species accomplished the dispersal.

Germain clearly considered that it belonged to Ariophantidae-Durgellinae but Thiele (1931, 1(2), p. 574) treated it under *Philalanka* Godwin-Austen, 1898 in the Endodontidae. Zilch (1959, 2, p. 220) follows the same course. With the permission of M. S. Tillier I extracted a radula from one of Germain's syntypes. A preliminary soaking in disodium





Fig. 2. Distribution of *Prositala butumbiana* (von Martens) superimposed on a map showing probable extent of forest during a pluvial maximum. (Simplified from a map by R. H. Carcasson deduced from the present distribution of butterflies).



hydrogen phosphate was made to soften the dried animal remains but no details of the anatomy could be made out. The radula is, however, undoubtedly endodontoid. The jaw consists of 15 joined plates transversely striate posteriorly (Fig. 1B). The radula is remarkable for the narrowly oblong multicuspid marginal teeth (Fig. 1C). Godwin-Austen (1897, p. 11–13) has discussed *Philalanka* and figured its anatomy. The radula shows some similarities to that of *Prositala* but differs in the shape of the marginals. The shell sculpture is widely divergent. I consider the two can be maintained as separate genera but until *Prositala* has been dissected it is not possible to confirm their relationships; I suspect they are abundantly distinct and that *Prositala* is isolated.

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PLATE 14

*Prositala butumbiana* (von Martens). Scanning electron micrographs of shell a $\times$ 25; b $\times$ 145; c $\times$ 1085 and d $\times$ 3625.

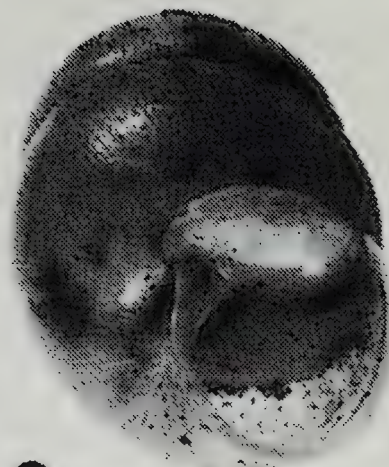




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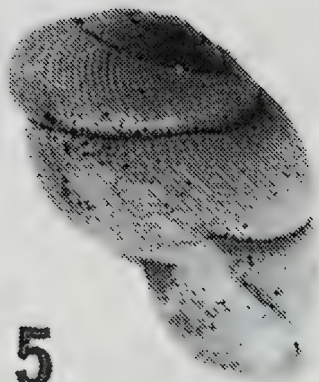
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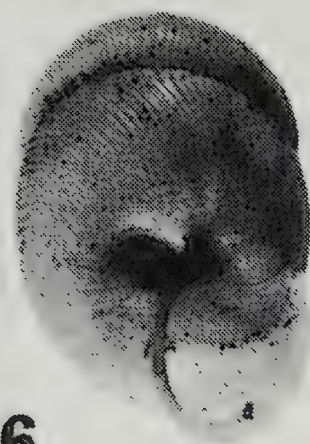
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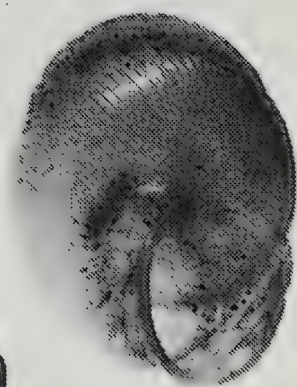
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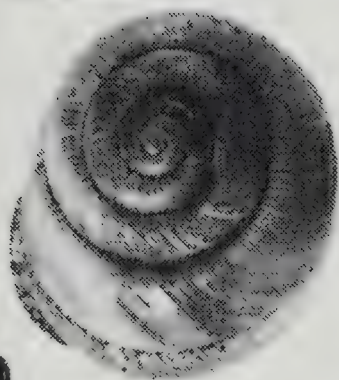
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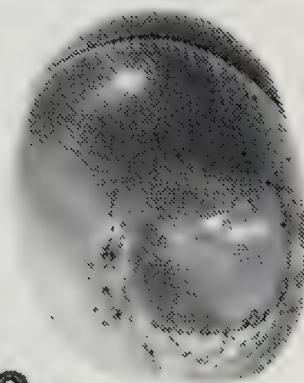
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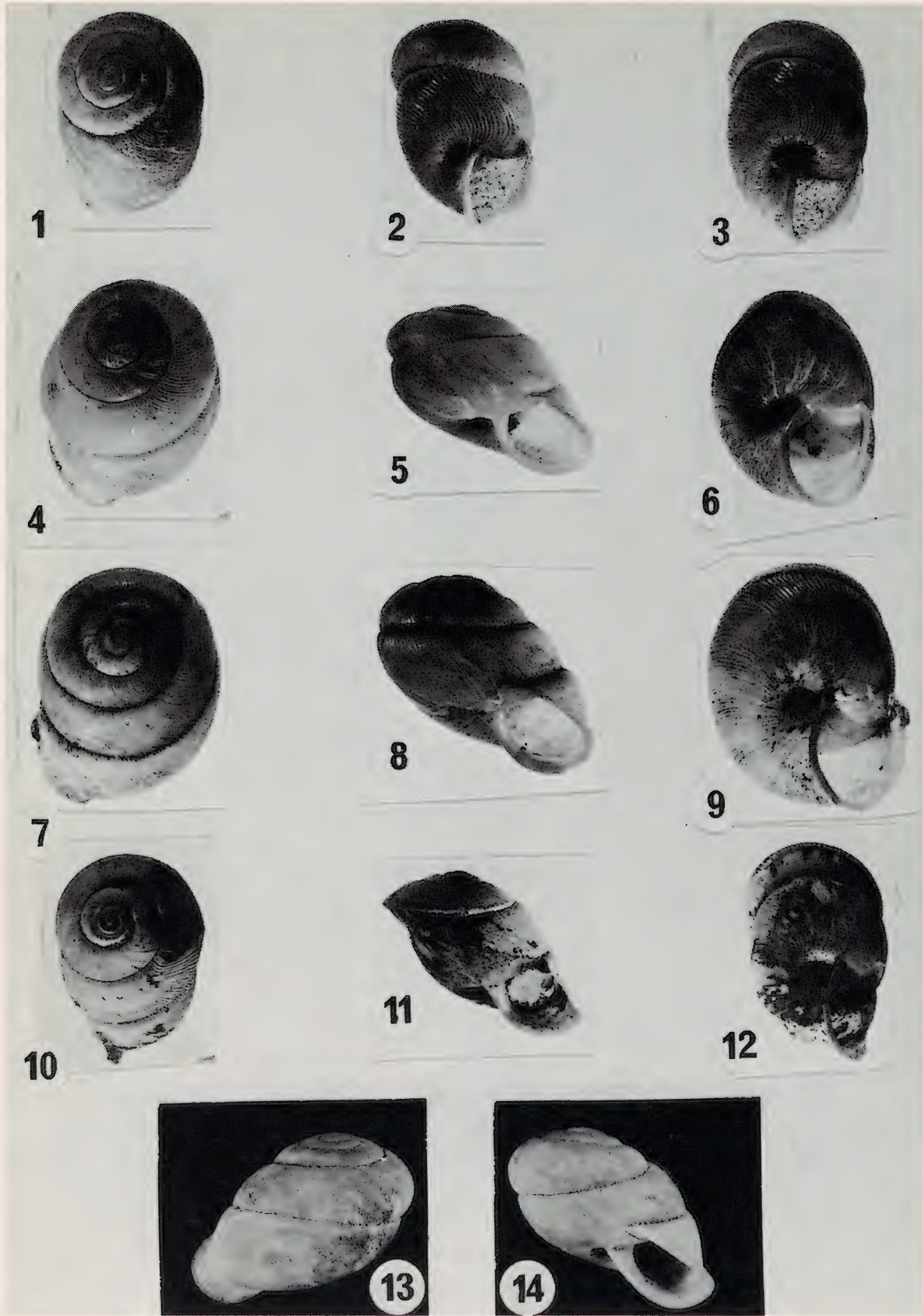


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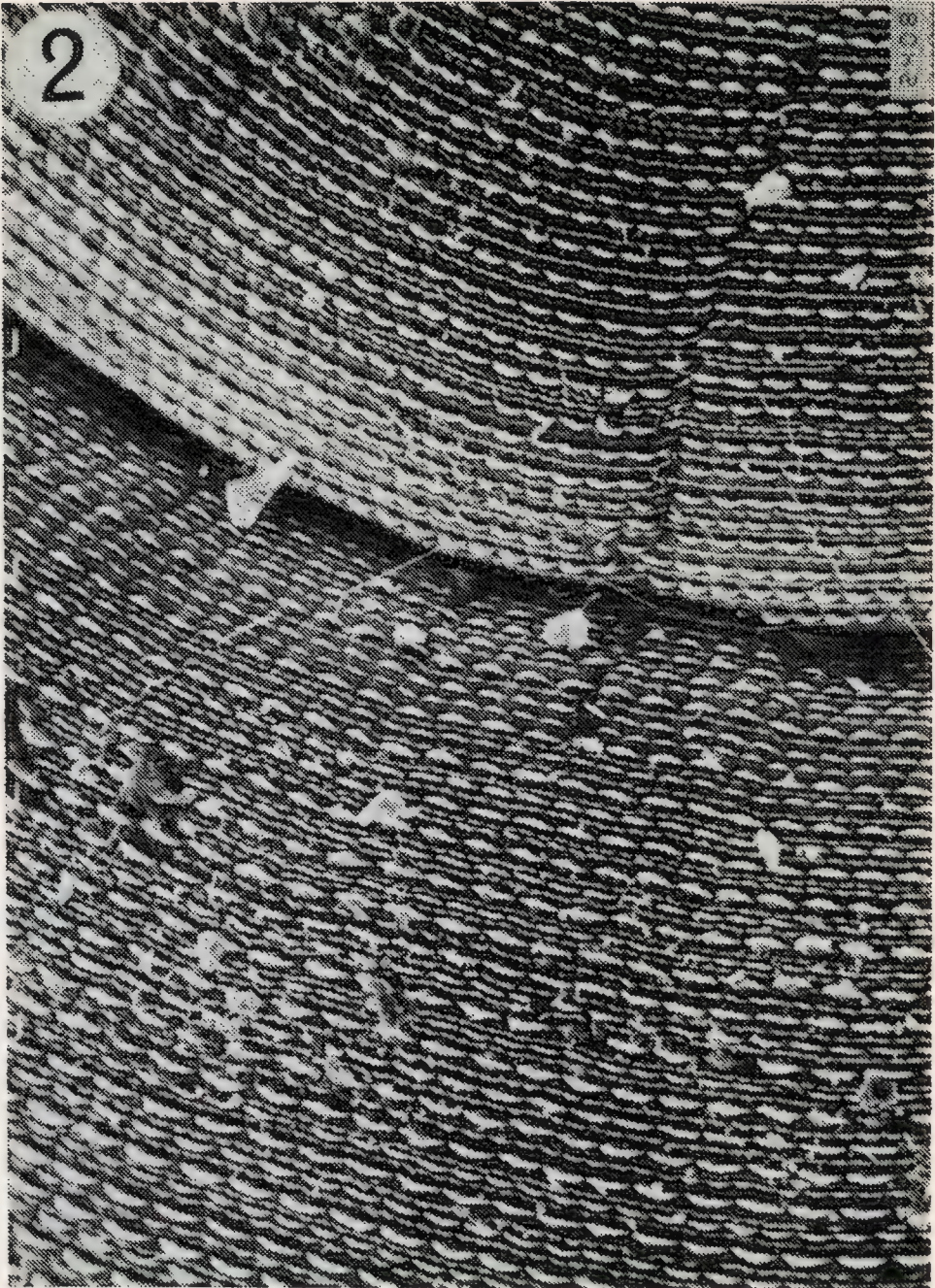
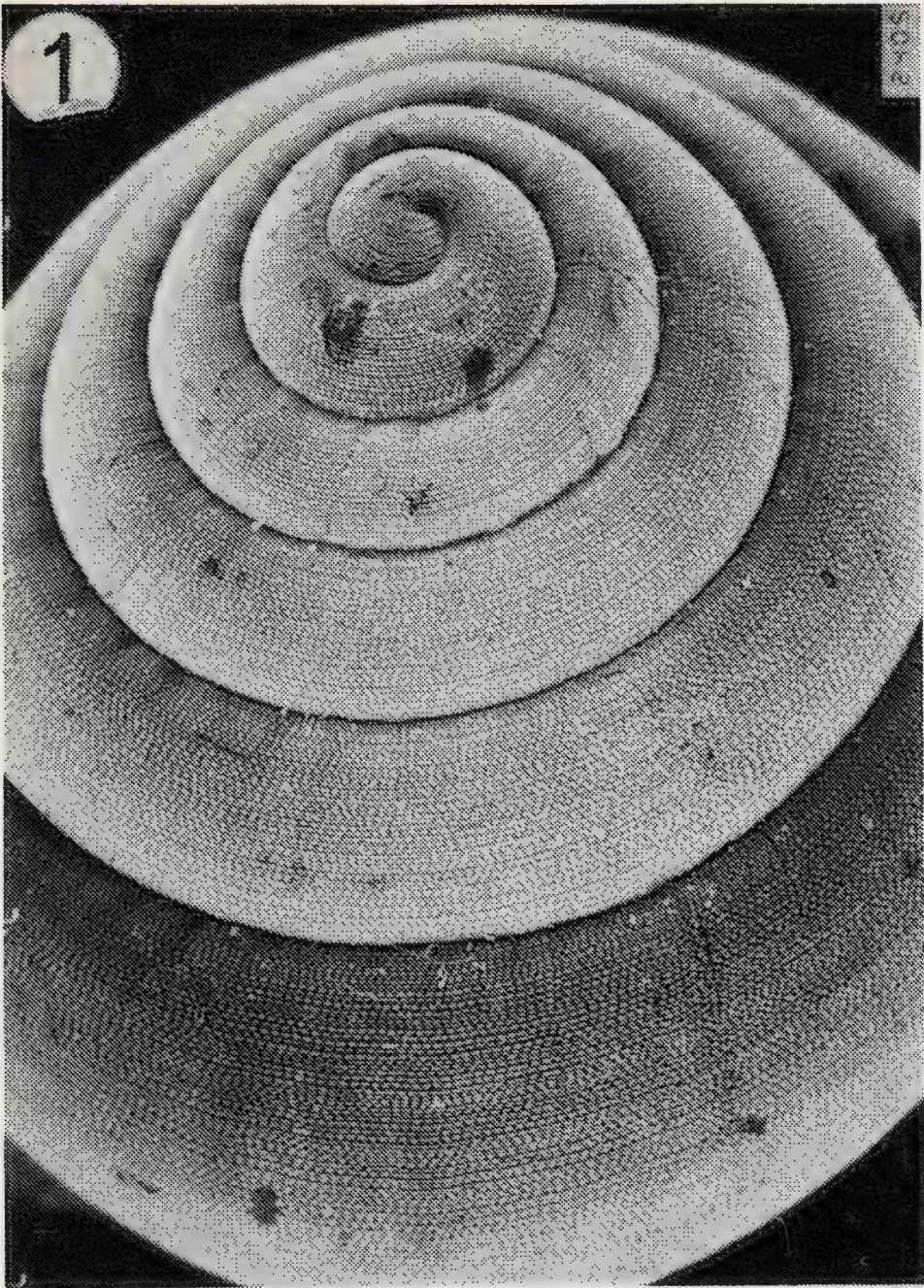


12















# THE INHERITANCE OF A SHELL COLOUR POLYMORPHISM IN *ACHATINA FULICA* BOWDICH FROM EAST AFRICA

JOHN A. ALLEN\*

(Accepted for publication, 15 May 1982)

*Abstract:* Some populations of *Achatina fulica* in Tanzania consist of snails with shells that are either streaked (*hamillei*) or unstreaked (*rodatzi*). The segregations of the two forms in the progeny of fourteen matings suggest that the presence of streaks is determined by a gene dominant to one for their absence. This shell colour variation is best interpreted as an example of genetic polymorphism.

## INTRODUCTION

Verdcourt (1966) recognizes two forms of *Achatina fulica rodatzi* Dunker (Pulmonata: Achatinidae), the coastal race of the Giant African Snail in east Africa. One, forma *hamillei* has a shell with dark brown streaks or flammules on a white ground. The streaks run transversely across the whorls and in many specimens there is a tendency for them to fuse together on the younger whorls. Forma *rodatzi*, on the other hand, lacks all trace of brown pigmentation but otherwise appears identical to *f. hamillei*. Verdcourt therefore supports Bequaert (1950) and Forcart (1961) in believing that *rodatzi* and *hamillei* are varieties of the same (sub)species.

I have collected eight random samples of live *A. fulica* from coastal Tanzania (Table 1). All the populations were living in areas disturbed by some form of cultivation. Six (from sites located within 20 km of the city of Dar es Salaam) consisted of *hamillei* alone, while the remaining two (one from the grounds of Tambaza School, Dar es Salaam; the other from a raised circular flower bed outside the Cathedral, Zanzibar) were mixed. The two forms differed not only in the presence and absence of streaks but also in the colour of the periostracum: yellow in *rodatzi* and yellow-brown in *hamillei*. Dissection of twenty adult snails from the mixed populations did not reveal any consistent anatomical differences between *rodatzi* and *hamillei*. In captivity the two forms mated freely and showed no discernible loss of fecundity or viability of progeny, when compared with homogamic matings. I conclude that Verdcourt (1966) is correct in assuming that *rodatzi* and *hamillei* are conspecific and I present data below to show that the variation is inherited in a simple Mendelian manner.

## MATERIALS AND METHODS

The snails for the breeding programme were collected in early 1974 from three of the populations listed in Table 1: Tambaza School, Zanzibar and the main campus of the University of Dar es Salaam. All the snails had a shell height of less than 30 mm and were judged to be immature (and therefore virgin). They were kept in the author's office in the Department of Zoology, University of Dar es Salaam and were reared as pairs in 2-l plastic beer mugs which were half-filled with soil and covered by sheets of glass. The soil was kept moist and calcium carbonate (usually in the form of crushed mortar) was added periodically.

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TABLE 1

Proportions of *rodatzi* and *hamillei* in eight populations of *A. fulica* in Tanzania (seven from near Dar es Salaam on the mainland and one from Zanzibar Island).

Locality	Year of sample	Numbers of:	
		<i>rodatzi</i>	<i>hamillei</i>
Kinondoni 1	1972	0	31
Kinondoni 2	1972	0	40
Zanzibar	1974	8	20
Tambaza School	1974	19	49
University Campus	1974	0	152
Ubungo	1975	0	67
Wazo Hill	1975	0	23
Kunduchi	1975	0	16

Each sample was collected by removing all the snails from a randomly chosen circular area of approximately 3 m radius. All samples were collected during the 'long rains' (March-June). *A. iredalei* Preston was also present in the Zanzibar locality.

Food was provided daily and consisted of either lettuce, cucumber, cabbage, chinese cabbage, carrot, squash or pawpaw. As the snails grew the glass had to be weighted down to prevent their escape.

All fourteen pairs (Table 2) were observed copulating between April and June 1974 (that is, during the main annual rainy season). Eggs began to be laid in the soil from June onwards but it was impossible to tell whether they had been laid by one or both partners in any given pot. Each batch could consist of over 100 eggs and therefore it was only practicable to rear (in a 2-l pot separate from their parents) one such batch per cross. All the crosses produced viable eggs. The young snails were reared under similar conditions to the adults but as they grew they were subdivided into a variety of larger containers (aquaria, dustbins, etc). The batches were scored for shell colour once the snails had reached a shell height of about 20 mm.

The original intention was to continue the breeding programme with twenty pairs set up from the progeny of the first fourteen crosses. These new pairs were transferred to the U.K. in 1976, but for some unknown reason never bred.

## RESULTS

The data for the fourteen crosses are given in Table 2. In spite of the early end to the breeding programme it is quite clear that *rodatzi* is determined by a gene recessive to one for *hamillei*. The results are in agreement with matings between the following pairs of genotypes: homozygous *hamillei* × homozygous *rodatzi* (crosses 7, 9, 10, 13), homozygous *rodatzi* × homozygous *rodatzi* (5, 6, 11), homozygous *hamillei* × homozygous or heterozygous *hamillei* (8, 14), heterozygous *hamillei* × homozygous *rodatzi* (3, 4, 12) and heterozygous *hamillei* × heterozygous *hamillei* (1, 2). None of the data for the last two types of mating depart statistically significantly from the expected 1:1 and 3:1 ratios (Table 2).

## DISCUSSION

*Rodatz*i and *hamillei* appear to be genetic variants of a single species, *Achatina fulica*. Moreover *rodatzi*, where it occurs, is at frequencies higher than would be expected if it were maintained



ALLEN: SHELL COLOUR POLYMORPHISM IN *ACHATINA FULICA*

TABLE 2

Results of *A. fulica* breeding experiments.

Cross no	Provenance	Parents	Progeny:		Expected ratio	$\chi^2$	P
			nos. of <i>rodatzi</i>	nos. of <i>hamillei</i>			
1	Z Z	<i>hamillei</i> <i>hamillei</i> ]	20	72	1:3	0.52	not significant
2	Z Z	<i>hamillei</i> <i>hamillei</i> ]	33	121	1:3	1.05	not significant
3	Z Z	<i>hamillei</i> <i>rodatzi</i> ]	61	51	1:1	0.89	not significant
4	Z Z	<i>hamillei</i> <i>rodatzi</i> ]	01	84	1:1	1.56	not significant
5	Z Z	<i>rodatzi</i> <i>rodatzi</i> ]	117	0	1:0	—	—
6	Z Z	<i>rodatzi</i> <i>rodatzi</i> ]	76	0	1:0	—	—
7	Z T.S.	<i>hamillei</i> <i>rodatzi</i> ]	0	163	0:1	—	—
8	Z T.S.	<i>hamillei</i> <i>hamillei</i> ]	0	95	0:1	—	—
9	Z UDSM	<i>rodatzi</i> <i>hamillei</i> ]	0	129	0:1	—	—
10	Z UDSM	<i>rodatzi</i> <i>hamillei</i> ]	0	84	0:1	—	—
11	T.S. T.S.	<i>rodatzi</i> <i>rodatzi</i> ]	75	0	1:0	—	—
12	T.S. T.S.	<i>hamillei</i> <i>rodatzi</i> ]	82	69	1:1	1.49	not significant
13	T.S. UDSM	<i>rodatzi</i> <i>hamillei</i> ]	0	153	0:1	—	—
14	T.S.	<i>hamillei</i> <i>hamillei</i> ]	0	140	0:1	—	—

The values of  $\chi^2$  are for the deviation of the observed results from the ratio expected on the assumption that *rodatzi* is controlled by a gene recessive to one for *hamillei*. All *rodatzi* shells were unstreaked with a yellow periostracum and all *hamillei* shells were streaked with a yellow-brown periostracum.

Abbreviations: Z, Zanzibar; T.S., Tambaza School; UDSM, University of Dar es Salaam.

in the populations by mutation pressure alone (Table 1). It seems probable, therefore, that the shell colour variation in *A. fulica* is an example of genetic polymorphism (Ford 1940), a phenomenon that is particularly widespread in pulmonate molluscs (Murray 1975, Clarke *et al.* 1978). This type of dimorphism for streaked and unstreaked forms occurs in other species of *Achatina* (Bequaert 1950, personal observations) as well as in members of the related genus, *Limicolaria* (Crowley and Pain 1970, personal observations). As far as I am aware, nothing is known of the inheritance of the colour forms in these snails. However, we do have some knowledge of the genetics of three highly polymorphic species of *Limicolaria*: *L. flammulata* (Pfeiffer), *L. aurora* (Jay) (Barker 1968, 1969) and *L. martensiana* Smith (Allen unpublished). These all possess a wide array of variants based on presence or absence of streaks, ground



colour, streak colour and streak pattern, and in all three absence of streaks is again controlled by a recessive gene. This is not necessarily a reflection of the close phylogenetic relationship between *Achatina* and *Limicolaria*, because it appears to be a general rule in pulmonates (with the exception of European helicids of the genus *Cepaea*) that presence of streaks or bands is controlled by an allele dominant to one for their absence (Clarke *et al.* 1978).

The present data do not indicate whether the unstreaked forms in the Zanzibar and Tambaza School populations are controlled by identical genes, and there is no hint whether a single locus is responsible for both presence/absence of streaks and periostracum colour or whether two tightly linked loci are involved. It had been hoped that the second wave of (unsuccessful) crosses would shed light on these problems.

With regard to the selective forces that act on the polymorphism, we can surmise that predation and climate may both play a role, as seems to be the case in other terrestrial molluscs (Jones *et al.* 1977, Clarke *et al.* 1978). In appearance, the two morphs are essentially dark or light (as a result of the presence or absence of streaks coupled with the colour of the periostracum) and therefore may well differ in, for example, their degree of crypsis and thermal properties in a given habitat. Relative differences in crypsis have been implied for the morphs of *Limicolaria martensiana*, the only achatinid whose ecological genetics have been studied in detail in the field (Owen 1963, 1965a, b, 1969). Five morphs were described by Owen (1969): streaked, unstreaked or 'pallid 3' (usually yellowish) and three other 'pallid' forms with pale or shortened streaks. The streaked form was recorded in all of the forty-nine Ugandan populations that were sampled by Owen (1969) and in thirty-two of them it was the commonest of the five morphs. The unstreaked form, on the other hand, occurred in only twenty populations, in sixteen of which it was the rarest morph. There was no good evidence for the sort of correlation between morph frequency and habitat type that has been reported for other land snails (reviews: Jones *et al.* 1977, Clarke *et al.* 1978)—perhaps because the habitats of *L. martensiana* are all rather similar, at least in colouration. Owen (1963, 1965b, 1969) has suggested that his data support the belief that in most places the streaked snails appear (to the human eye) the most cryptic. Other things being equal, the pallid morphs in any one population should then be more likely to be detected by predators hunting by sight and their frequencies should fall accordingly. One possible explanation why they persist at low frequencies in many populations is that even though they may be relatively more conspicuous they tend to be overlooked by predators that search preferentially for the common forms. Such 'apostatic selection' (Clarke 1962) can result in the maintenance of genetic diversity and is likely to be progressively more effective (to a point) as prey density increases (see, for example, Cook and Miller 1977). If apostatic selection does indeed operate on *L. martensiana* then the degree of polymorphism in a population might be expected to be directly related to population density, which in fact is just what Owen (1963, 1965b) has claimed to have found.

Snails of the genus *Limicolaria* are absent from the coast of east Africa (Crowley and Pain 1970). Polymorphic populations of *A. fulica* are probably uncommon but widely distributed throughout the region (Verdcourt 1966, personal observations) and it would be instructive to discover whether this species follows the trends found in *L. martensiana*. In other words, is the unstreaked form generally the rarer (and the more conspicuous) of the two morphs and is there a positive relationship between polymorphism and density? Predators of *A. fulica* certainly abound in east Africa (Williams 1951, Mead 1960, 1978, Kasigwa *et al.* 1983), but we have no data to suggest that any of them prey selectively on the morphs. Climatic factors, such as temperature, were neglected by Owen in his search for the selective forces acting on *L. martensiana* but these have since provided a profitable area for research on other polymorphic land snails (Jones *et al.* 1977, Clarke *et al.* 1978). The large size of *A. fulica* makes it ideal for field and laboratory experiments designed to test for ecophysiological differences between the morphs.



*A. fulica* is no longer confined to its east African homeland (Mead 1960, 1978). It is found on many islands and continents in and around the Indian and Pacific Oceans and some of these populations could conceivably be polymorphic for streaked and unstreaked forms. This highly successful mollusc demands a lot more attention if we are ever to unravel the factors that act to maintain and decrease its degree of polymorphism for shell colour.

#### ACKNOWLEDGEMENTS

In particular I thank the Department of Zoology, University of Dar es Salaam, for providing space and manpower for maintaining the snails. I also thank the Department of Zoology, Reading University and the Department of Biology, University of Southampton in a similar context. Jon Cooper, Simon Lawrence and Debbi Raymond criticized the manuscript while Karen Pimlott and Sue Coxson typed it.

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## COMMUNICATIONS

### A QUICK SECURE WAY OF MARKING FRESHWATER PEARL MUSSELS

In an ecological study we needed a method of marking individually freshwater pearl mussels which was quick, clear and secure for some years. After unsuccessful trials with engraving numbers (erosion resulted), painting numbers (they wore off) and tags applied with epoxy-resin glues (too slow to set), the following method was devised.

Each mussel was removed from the water and dried roughly. An area of about 10×5 mm on the flattest part of the shell (usually  $\frac{2}{3}$  of the way between the shell edge and the umbone and near the anterior end) was scraped clean of periostracum with a scalpel. This area was dried with a tissue and then wiped with a tissue soaked in 100% alcohol. This was allowed to evaporate and then a tag was stuck on with a small amount of 'Loctite' or other 'superglue', allowing 30 seconds pressure for the glue to dry. The tags were made from Dymo tape cut as small as possible around the impressed numbers and with the corners rounded off. The whole procedure takes about two minutes.

In a typical trial 20 mussels were marked and returned to their stream in June 1978. One died in July 1979, with its mark intact, and by March 1981 18 of the remaining 19 still had secure tags. In many of our experiments not a single tag was lost and no casualties resulted.

M. R. YOUNG and J. C. WILLIAMS

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### LAND MOLLUSCA FROM NORWAY, SWEDEN AND FINLAND

Various land Mollusca found in northern Fennoscandia during July–September 1982 represent new distributional records. Most of these are to the north of the northern range limits described in the literature (*Skr. norske Vidensk. Akad.* 1 (1925), p. 8; *Ann. Zool. Fennici* 4 (1967), p. 29; Kerney & Cameron, *A Field Guide to the Land Snails of Britain and North-west Europe*).

*Arion circumscriptus* Johnston. North-east of Umeå, Sweden (UTM grid reference: DR78).

*Arion silvaticus* Lohmander. Some records are to the north of the range limits hitherto reported: Norway (DC21), Sweden (CR92, DR35), Finland (NL95, PK49).

*Arion distinctus* Mabilie. Small plantation of *Acer*, *Picea* and *Betula* in Stokkmarknes, Hadselöya, Norway (VS90). At 68° 34' N. this is far to the north of the range limit reported at around 63° N. for the *Arion hortensis* Férussac aggregate.

*Oxychilus draparnaudi* (Beck). Under herbs on rockeries, Bergianska Trädgården (botanic garden), Stockholm (CL83). Waldén (*Ark. Zool.* (2) 7 (1955), p. 412) confirmed only one other record from the Stockholm region.

*Limax maximus* L. Beneath garden refuse under trees by graveyard at Karjalohja, Finland (FM58). There does not appear to be any other record from an open site in Finland, although it is not rare in greenhouses (*Ann. Zool. Fennici* 4 (1967), p. 31).

*Clausilia bidentata* (Ström). Several sites in Troms Fylke (DC72, EC05) are near the north-eastern range limit reported in Norway. However, a site 2 km WSW. of Borselv, east Porsangen (MU04) is the first record from Finnmark and over 300 km to the east of the range limit hitherto known. At the Porsangen site it was living under *Betula pubescens* Ehrh. amongst boulders at the base of a limestone crag.

*Balea perversa* (L.). Several records extend the northern range limit in Norway beyond the 68° N. hitherto reported (VR24, VR35, VR58, VS80, WS04, WT80, CC82). All of these northern sites were on rocks 3–12 m above high-tide level on shores exposed to the west. The snails occurred along the edges of rock cracks beside *Festuca rubra* L. and herbs, or under the edges of moss mats (principally *Racomitrium*). The northernmost record was on the west coast of Store Sommaröya, west of Tromsö at 69° 38' N.

*Trichia hispida* (L.). A thriving colony living on *Heracleum sphondylium* L. and other herbs growing on waste ground near the south end of Strandvegen in Tromsö town (DC22) at 69° 38' N. is beyond the range limit hitherto reported, although this site resembles others reported from the northern part of the range in being associated with man. However, several other records from northern Norway are from habitats undisturbed by man, including a grove of *Alnus incana*, *Salix* and *Betula* (XR09), amongst herbs and grasses on limestone cliff at edge of fiord (WS61) and block scree shaded by *Betula*, *Sorbus aucuparia* L. and varied tall herbs (VR87).

We wish to thank the NERC for research funding and M. Holyoak for field assistance.

D. T. HOLYOAK and MARY B. SEDDON

University of Reading, 2 Earley Gate, Reading RG6 2AU.



## COMMUNICATIONS

### A SECOND BRITISH FOSSIL OCCURRENCE OF *LYRODISCUS* (FAMILY ZONITIDAE)

In 1976 Dr. M. P. Kerney described an interglacial molluscan fauna probably of Hoxnian age from a tufa near Icklingham, Suffolk (*J. Conch., Lond.* **29**, p. 47). The fauna included a new zonitid, *Retinella (Lyrodiscus) skertchlyi*. *Lyrodiscus* today lives only in the Canary Islands but the taxon was formerly widespread in Europe. Similar shells have been found in Pliocene and Early Pleistocene deposits in southern France, Germany and the Netherlands (*Conchologists' Newsletter* no. 72 (1980), p. 217).

*Lyrodiscus* can now be reported from a second British site—Sunhole, a small fissure cave at Cheddar Gorge in Somerset (ST 467541). Five fragments showing the highly characteristic spiral sculpture were recovered from layer 35 of Colcutt *et al.* (*Proc. Univ. Bristol Spelaeol. Soc.* **16** (1981), pp. 21–38). The associated mammals appear to indicate a Hoxnian age (Dr. A. P. Curren, *personal communication*). This layer is stratigraphically lower than the layer which yielded the Postglacial mollusc fauna described from Sunhole by Davis (*ibid.* **7** (1955), p. 71).

I should like to thank Dr. Kerney for identifying the *Lyrodiscus* fragments.

CAROLINE ELLIS  
Imperial College, London SW7 2BP.

## DONATION

The Trustees of the Society acknowledge the receipt of a Certificate for £2,200 10¼% Exchequer Stock 1995 given 'in lieu of a legacy'. The Council for the Society at its meeting on 19 February 1983, unanimously passed a resolution of most grateful thanks to the Donor.

## NOTICE

While the Journal was in press, the Council of the Society heard of the death, on the 27 February, of *Arthur Erskine Ellis*. An obituary will appear in a future issue of the Journal.







## INSTRUCTIONS TO AUTHORS

Manuscripts should be sent to:— **Dr M. P. Kerney, Department of Geology, Imperial College, London SW7 2BP.**

**PAPERS** Two copies of text and illustrations should be submitted; one set of illustrations must be good quality originals. Authors should refer to recent copies of the *Journal* for a guide to format. Authors are reminded of the high cost of printing and therefore are expected to write concisely and to make maximum use of page size when designing art-work and tables.

**COMMUNICATIONS** These are intended to be short notes of an original nature which do not merit the treatment of a full paper. *Communications* must not contain any figures, tables or plates and should conform in style to that of recent issues of the *Journal*.



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*A. E. Ellis*

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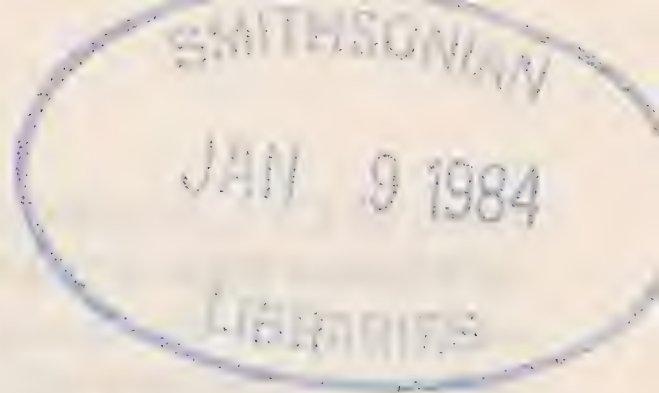
PLATE 15

ARTHUR ERSKINE ELLIS (1902-1983)









## OBITUARY

### ARTHUR ERSKINE ELLIS (1902-1983)

Arthur Ellis died suddenly, in his sleep, at Alphington, Exeter, on the 28th February 1983. Before his death he left biographical notes for his obituary with Dr. Paul, then *Honorary Editor* of the *Journal of Conchology*. His letter to Dr. Paul and his biographical notes require little comment and are reproduced here essentially unchanged except for bringing the bibliography up to date and with the addition of an appraisal from Terry Crowley.

7 St. Michael's Close  
Alphington  
Exeter 14 Jan. 1976

Dear Dr. Paul,

One of the headaches of an editor is the writing of obituaries of members of the Society on the melancholy occasions when this duty becomes due. I once inserted an appeal to members to let me have biographical particulars so that these notices might be accurate and according to the wishes of the subject. I had three responses, I believe. Either people are too modest, or else have a morbid fear of anticipating the inevitable. I think I did provide Heppell with biographical particulars some years ago, but they are now probably lost, and in any case a bit out of date. I am therefore sending you the story of my life and list of publications, on which the writer of my obituary will be able to draw. I did supply such particulars to the Linnean Society (which no longer publishes obituaries), but this provided the material for an advance in *Biol. J. Linn. Soc.* 2:326. Few people are privileged to read their own obituary in advance! Perhaps this document can eventually be placed with the Society's archives.

I am also sending the last studio portrait I had taken, about 30 years or more ago I think.

Yours sincerely

A. E. Ellis

In common with all biographies, the really interesting parts are omitted of course!

#### ARTHUR ERSKINE ELLIS: BIOGRAPHICAL NOTES

*Born* at Bangalore, India, 1st October 1902.

*Father*: Robert Arthur Ellis, Wesleyan Methodist Minister (obituary in the *Minutes of the Methodist Conference*, 1963, p. 185), author of *Spiderland* (Cassell, 1912) and articles on natural history, chiefly in the Magazine of the Wesleyan Methodist Church. All photographs illustrating the works of AEE were taken by RAE, who had been a keen and expert photographer since his student days at Richmond College. He was a son of Robert Powley



Ellis, M.C.O., Superintendent of the Line, Great Eastern Railway. The family is traced back to Richard Ellis of Polebrook, Northants., early seventeenth century. The name Erskine is derived from Sir David Erskine, son of the eleventh Earl of Buchan, who married Anne Ellis—the family's only brush with the nobility; it does, however, include a suspected murderer and its quota of drunkards.

*Mother:* Mary Ellis (née Gardner), M.B., Ch.B. (Glasgow). She entered Glasgow University the year degrees were first conferred on women.

*Places of residence:* being a Methodist minister, RAE moved frequently, starting at Taunton on returning from India, then Radcliffe-on-Trent; Triangle, near Sowerby Bridge; Chippenham; St. Just-in-Penwith; Market Harborough; Ampthill; Haverfordwest; Attleborough, Norfolk. He retired in 1932 and lived at Thorpe St. Andrew, till 1951, then at Carshalton, Surrey. Mary Ellis died in August, 1951, and RAE on St. Luke's Day, 1962, in his ninetieth year.

*Education:* Sowerby Bridge Secondary School, 1910–12.

Kingswood School, Bath, 1912–21. The pass mark for the entry examination was 80 out of 200: AEE just scraped through; after one term at K.S. was third from bottom of the school, where he had an undistinguished career. Quotes from early reports: 'Owes his position to native wit rather than industry;' 'Laziness is spoiling his work.' This has always been a besetting failing, inherited, his mother averred, from her Irish father.

School Prefect, 1919; Second Prefect and Head of House, 1920. Apart from a prize for French in the Lower Fourth, won no prizes involving work: Gabriel Prize for natural history, 1920 & 1921; Punshon Prize for reading, 1921. Received an old fashioned classical education and did no science at school, being considered too weak at mathematics—besides, the 'modern side' was looked down upon,—but whole life changed in his final term by winning the Gabriel Prize. This came to the notice of Frank Potts, Trinity Hall, Cambridge, University Lecturer in Zoology, an Old Boy and Governor of Kingswood, who happened to visit the school at that time. He recommended AEE to take Biology instead of English at Oxford, so an eleventh hour switch was made. The obstacle was the necessity of passing the Preliminary Examination in Physics and Chemistry, subjects of which AEE was entirely ignorant (he did not even know what Physics was about), but the Prelims. in Physics & Chemistry and in Zoology & Botany were passed in the first year at Oxford. An incalculable debt of eternal gratitude is owed to Potts, who has since been venerated like a patron saint.

*Oxford:* St. Edmund Hall, 1921–25. Christopher Welch Scholarship, 1925. First Class, Honour School of Natural Science (Zoology), 1925. B.A., 1925; M.A., 1933. Secretary of Oxford University Junior Scientific Club, 1924 (declined presidency). President of St. Edmund Hall Essay Society, 1925.

Whole career shaped by the good fortune of being useless at games and sport, which left one free as a prefect at Kingswood to explore the country round Bath on an ancient bicycle, and to extend the study of Biology at Oxford beyond the laboratory.

*Posts:* Biology master at Lancing College, 1925–31. This was another critical stroke of fortune: the Principal of St. Edmund Hall happened to be visiting the Headmaster of Lancing, when the latter casually observed that he was starting biology in the school next term (the subject was taught in very few schools then) and wanted a teacher. 'I have the very man,' replied Dr. Allen, 'he has just won a university research scholarship and is bound to get a first.' The upshot was that while in bed with 'flu AEE got a telegram from Canon Bowlby summoning him to Lancing.

Head of Biology Dept., Epsom College, 1931–63. This was another random chance: the school secretary happened to remark that he had seen the post advertised, so as the salary offered was twice what AEE was then getting, he applied.

Examiner in Biology (Premedical) to the Royal College of Surgeons for eleven years.

Fellow of the Linnean Society, 1931. H. H. Bloomer Award, 1970.



## OBITUARY

Fellow of the Zoological Society. Stamford Raffles Award for 1974.

Member of Malacological and Botanical Societies (member of Council and vice-president for former).

Conchological Society, 1923; President, 1939–41; Recorder of non-marine Mollusca, 1948–61; Editor of *Journal of Conchology*, 1948–64; Curator, 1964. [Honorary Membership of the Conchological Society, 1976.]

First interest was butterflies and moths, then plants, of which a comprehensive herbarium was amassed over 40 years (this is now at Lancaster University); botany has shared equal place with conchology in his interests and enthusiasm. Later on took up various small groups, such as dragonflies, ants, harvestmen, false scorpions, woodlice and Orthoptera (*sensu lato*). First became interested in freshwater Mollusca at Kingswood (*Conchologists' Newsletter* No. 1, p. 16) and in land Mollusca at Oxford, where he became friends with O. W. Richards (later Professor of Entomology at Imperial College), with whom collections were exchanged—AEE receiving OWR's land & freshwater shells, while OWR received AEE's Lepidoptera; the latter had the best of the exchange.

While at Lancing became friends with Ronald Winckworth, then living at Brighton, whose elder brother was a visiting violin teacher at Lancing. He was greatly helped and influenced by this remarkable man (see *J. Conch.* **23**:157). Other valued friends were G. C. Robson, A. E. Boycott, A. S. Kennard, and J. R. le B. Tomlin: their memory has always been precious.

*Collections*: the non-marine Mollusca, with which were incorporated those from Winckworth's collection, were presented to the British Museum (Natural History) in 1963. Collections of woodlice, harvestmen and false scorpions were given to the Dept. of Zoology, Oxford. Collections of dragonflies, Orthoptera and ants were left in the museum which AEE created at Epsom College.

*Species named after AEE*: *Limicolariopsis ellisi* Crowley & Pain, 1964 (*Rev. Zool. Bot. Afr.* **69**: 191).

*Pisidium (Afropisidium) ellisi* Dance, 1967 (*J. Conch.* **26**:178).

Contributed numerous plant records to Rep. Bot. Exchange Club, Wolley-Dod's Flora of Sussex, Horwood's Flora of Leics., and Druce's Flora of Northants. Discovered a sea lavender new to science, *Limonium paradoxum* Pugsley, 1931 (*J. Bot.* **69**: 44–47), and a new hybrid fumitory, *Fumaria officinalis* × *micrantha* (det. Pugsley). Specimens of *L. paradoxum* were presented to the Druce herbarium at Oxford.

In addition to the publications in the appended list, AEE wrote the section on non-marine Mollusca for the new edition of Farmer's Book of Nature Study, which never got beyond galley proofs. These were given to the Molluscan Library at the British Museum (Nat. Hist.) and subsequently lost.

## ARTHUR ERSKINE ELLIS: AN APPRAISAL

It was typical of Arthur Ellis that he should have written his own obituary, since he had a habit of accuracy which nothing could disturb. This to him was the mark of the scientist and certainly took precedence over popularity, expediency or the peaceful life. It was certain that he knew more about his own career than anyone else did, so he set it out fully for the use of future generations; and if they didn't want it, he would not have been in the least concerned.

His words were few and always carefully chosen: he rarely made an unsolicited remark except on a matter of importance, such as paying a compliment to a lady. Partly, this was the practice of a shy man and indeed, Ellis was not for everyone an easy man to know. Much of himself was deliberately hidden, but having passed this little barrier and found something in



common, you discovered that he had a rather rare genius for friendship, and would be happy to give, psychologically, more than he needed to take from you.

He never sought the limelight, this would not have been in accordance with his logical attitude: his term as President of the Society occurred during the dark days of the War, and nothing would induce him to take the Office again when meetings became so much better attended. It was with difficulty that he could even be prevailed upon to lecture the Society, and then only with the stipulation that all alternatives had been found wanting; but what a treat for members it was when he did. To learn from Ellis's lips about his own favourite freshwater bivalves (among many other things) was an intellectual joy. Those who studied under him at Epsom College seemed to have had a healthy awe of him but felt at the same time a great allegiance and agreed in calling him an unusually effective instructor.

He remarked that he left his profession without regrets, but later, after a temporary appointment at a girl's school, was heard to say that he had been wasting his time on horrid boys when he might have been teaching such attractive and delightful maidens. This may have been one of his occasional provocative remarks: Ellis has little use for humour in the restricted sense, but his wit was dry and could make the hearer squirm with delight. It was straight faced, bore not a trace of sarcasm or malice, and criticised no one (except sometimes, himself). Criticism was too serious a matter for wit, though he did not hesitate to criticise too, where he thought it deserved. To submit a paper to the *Journal* when he was editor was to take a risk. If he thought the work capable of improvement, either in matter or manner, back it would come, with a schoolmasterly note. References were always checked and if a quotation lacked so much as a comma, it was incorrect and had to be amended. Such a policy maintained a very high standard, both of the *Journal* and of those who wrote for it. Who could not improve under such an editor?

On the other hand, his book *British Snails* 1926, which was the standard work on the subject and the only up to date reference book for forty years, he dismissed as 'a youthful indiscretion'.

The character portrayed above does seem to come out as a rather arid individual, but in fact Ellis was far from that. No toffee-nose could have written half the things he did—his ghost stories, for instance, or his studies of poetry. His chief delight for many years was a field meeting to survey an area or seek a rarity with one or two friends, or even solo, finishing up in a cosy pub with a pint or two of ale—providing it was understood that there was to be no treating. This was another matter of principle.

The men who worked in the molluscan field during the reign of King George V laid the foundations of the subject which has now reached scientific refinement. The best of them were not only men who had an immense general knowledge of the whole subject (and usually others as well), but where themselves great characters, remembered for what they were as well as what they did. To some of us, joining the Society after the last War, Ellis seemed then like the last member of that great company. Thirty years later, that is how he appears still. Logic ruled his life but left much room for humanity as well.

T.E.C.

#### NON-MOLLUSCAN PUBLICATIONS:

- 1929 Birds at Lancing. *Lancing College Magazine* **22**:62–65.
- 1930 More Lancing Birds. *ibid.* **23**:2–4.
- 1929–30 Animal Associations. *School Science Review*, No. 41, pp. 31–38; No. 43, pp. 246–258; No. 45, pp. 43–54.
- 1942 The natural history of Wheatfen Broad, part 4. The woodlice and harvestmen. *Trans. Norfolk & Norwich Nat. Soc.* **15**:291–300.
- 1943 Miscellaneous observations: notes on Ampipoda, Oniscoida, Chelonethi, Opiliones, Orthoptera and Odonata. *ibid.* 372–374.
- 1943 Notes on the woodlice of Surrey. *Proc. Croydon Nat. Hist. & Sci. Soc.* **11**:152–153.
- 1943 Miscellaneous notes (Opiliones, Dermaptera). *ibid.* 153.



## OBITUARY

- 1948 The survey of Bookham Common. Woodlice of Bookham Common. *London Naturalist* for 1947: 59–60. *Ibid.*, Amphipoda: p. 60.
- 1948 Fauna and flora of Norfolk: miscellaneous observations. Notes on snails, amphipods, false scorpions, dragonflies and grasshoppers. *Trans. Norf. & Norw. Nat. Soc.* **16**:330–332.
- 1949 Flora and fauna in Dutt, W. A., *Norfolk* (The Little Guides), revised by E. T. Long (brother-in-law of AEE) pp. 15–19. Methuen & Batsford, London.
- 1965 Mollusca, Woodlice and Harvestmen (pp. 164–171) in Ellis, E. A., *The Broads*. The New Naturalist vol. 46. Collins, London.  
(Edward Augustus Ellis and Arthur Erskine Ellis are not related though often confused)

Articles contributed to the *Magazine of the Wesleyan Methodist Church*:

- 1925 vol. 148: Nature's Calendar, Jan., March, April, Dec.
- 1926 vol. 149: Nature's Calendar (all months), in co-operation with RAE.
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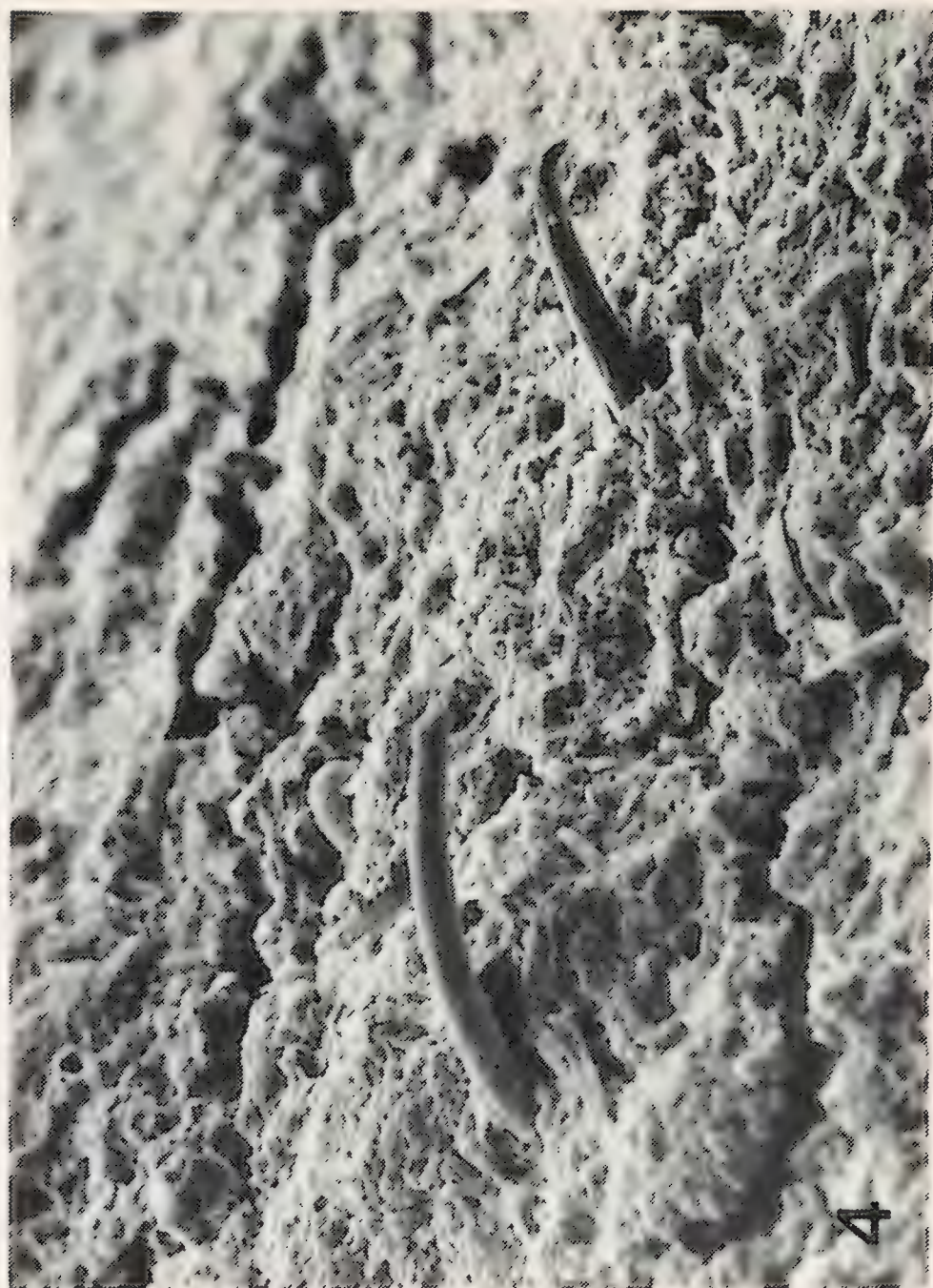


Plate 16.

Fig. 1. *Perforatella rubiginosa* dart tip  $\times 40$ . (one fin shows some damage). Syon Park, Middlesex. Fig. 2. *Ashfordia granulata* shell surface  $\times 100$ . Box Hill, Surrey. Fig. 3. *Perforatella rubiginosa* shell surface  $\times 100$ . South Stoke, Oxfordshire. Fig. 4. *Perforatella rubiginosa* shell surface  $\times 100$ . Syon Park, Middlesex.







# PERFORATELLA: THE HELICID SNAIL NEWLY RECORDED IN BRITAIN AND OTHER GENERA COMMONLY CONFUSED WITH *TRICHIA*

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(Accepted for publication 21 May 1983)

*Abstract:* Several taxa may be confused with species of *Trichia* in Britain including the recently identified *Perforatella rubiginosa*. Features of the genital anatomy provide a more reliable means of discrimination at generic level than do shell characters.

## INTRODUCTION

The status of small helicid land snails which possess a hairy periostracum and are widely distributed in damp habitats has continually caused problems for European malacologists. In Britain the main problem would seem to be the status of forms within the *Trichia hispida* (L.) and *Trichia striolata* (L. Pfeiffer) groups (Forcart 1965, Paul 1975, Kerney & Cameron 1979, Naggs 1982) but members of other genera possess shells sufficiently similar to *Trichia* for them to be confused, although they can be easily distinguished on anatomical grounds. That *Perforatella* has only recently been recognised in Britain (Verdcourt 1982, Naggs 1982, 1983,) serves to emphasise the need for attention to be drawn to these features.

## FEATURES OF THE GENITALIA

The most useful characters would seem to be those of the genitalia proximal to the genital orifice. On the assumption that these features are involved in species recognition they can be classed as 'privileged characters' when seeking to distinguish homology from convergence (Cain 1982). At any event they have been used to establish what are thought to be natural groups within the family Helicidae (Pilsbry 1894, Watson 1943, Shileyko 1978, 1979).

The genitalia are most easily examined in snails that have been killed in an extended state. This is usually achieved by narcotization (Runham *et al.* 1965) or by drowning in water that has previously been boiled to displace dissolved oxygen. Removal of the organs is then easily effected by cutting around the genital orifice, severing the penis and right eye retractor muscles and cutting through the spermoviduct above the spermatheca.

*Trichia* (Fig. 1) may be recognised by its possession of a pair of dart sacs each side of the vagina. In fact, the precise role of these sacs is not clear. In dissected specimens the internal sacs have no trace of a dart, and are usually termed accessory sacs, whilst the external sacs contain granular structures which fragment under the lightest pressure. Opening into the vagina above the dart sacs are more elongate and variable sacs, the mucus glands. Members of the *Trichia hispida* and *Trichia striolata* groups usually have four pairs of mucus glands, each pair joined at the vagina or attached to a short stalk. The vagina extends into a long tube, the spermatheca duct, which terminates in a bulbous sac, the spermatheca. Following copulation a spermatophore, contributed by the snail's partner, rests tightly pressed into the

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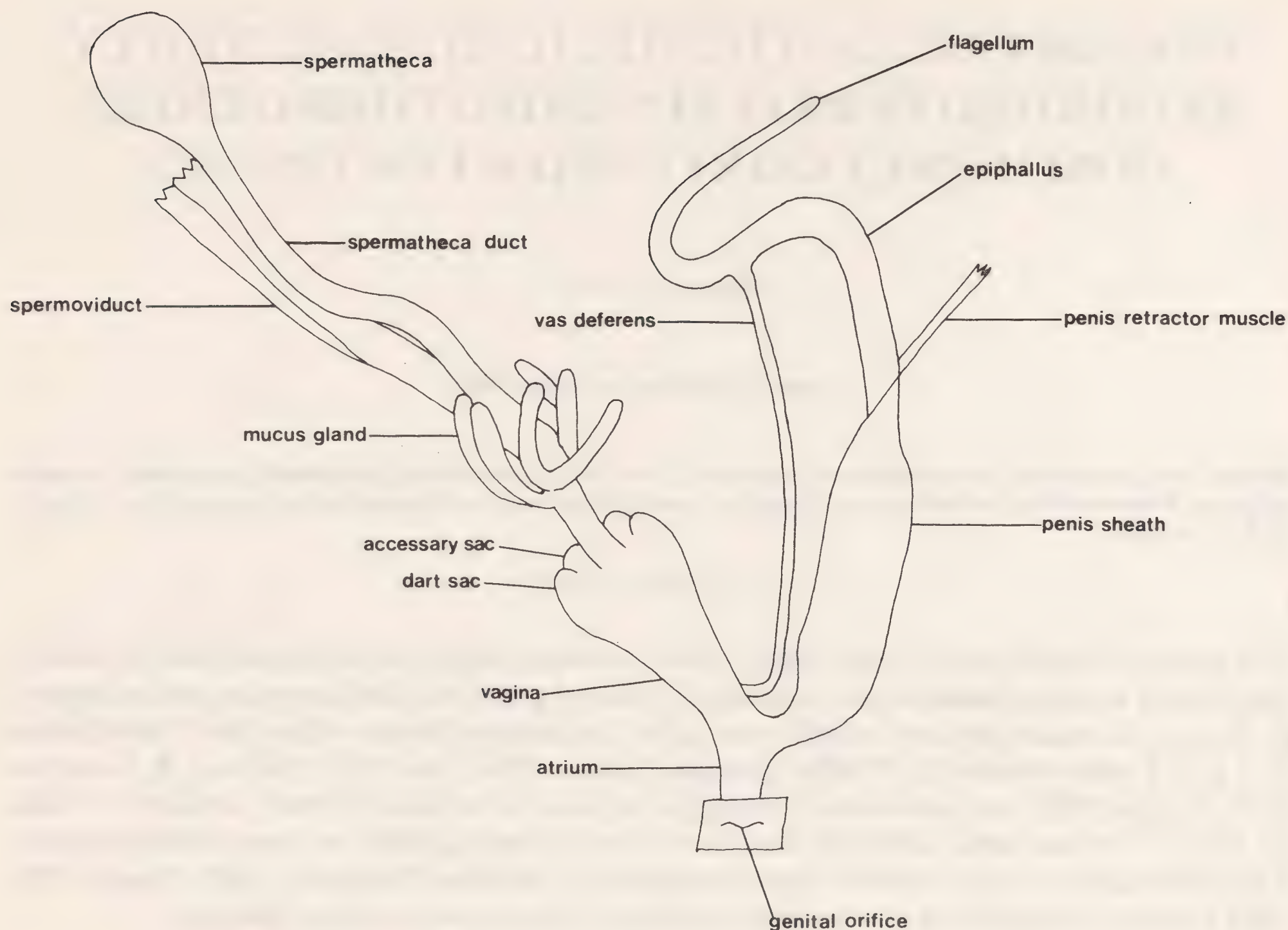


Fig. 1. Generalised *Trichia* genitalia proximal to genital orifice.

spermatheca with a long tail extending down the spermatheca duct into the vagina; the resulting distortion must be recognised if the gross structure of the spermatheca and spermatheca duct are to be used as taxonomic characters. The male half of the genitalia meets the vagina to form the atrium but the penis is usually hidden from view being enclosed within the penis sheath. Close to the insertion of the penis retractor muscle, the penis is attached to the inner wall of the penis sheath. From here the male duct extends back as an epiphallus to the junction of the vas deferens with the flagellum. Although the flagellum and epiphallus are the site of spermatophore formation this role is transitory, the spermatophore is probably formed only minutes before expulsion as is known to be the case with *Helix pomatia* (L.) (Lind 1973), and one is unlikely to be found here in preserved material.

Because *Ponentina subvirescens* (Bellamy) can be recognised externally by the green hue of its shell and by the peristome which is partly reflected over a narrow umbilicus, it is unlikely to be confused with the *Trichia* groups. The genitalia were described by Ellis (1926 p. 212): 'the dart-sacs are vestigial, the vagina and penis sheath swollen, and there is a pair of bifurcate mucus glands. The flagellum is short and stout, and the spermatheca oval, with a long duct'. Only the one species of this Atlantic seaboard genus is recorded from Britain but the forms occurring further south in its range, such as those mentioned by Gittenberger (1978) as occurring in Portugal, may represent several taxa.





Fig. 2. *Perforatella rubiginosa* genitalia. Specimen from South Stoke, Oxfordshire. March, 1983.

Continental *Perforatella* show a range of shell forms (Kerney & Cameron 1979) but only those known as *Perforatella rubiginosa* (Schmidt)<sup>1</sup> possess periostracal hairs and these snails are easily mistaken for *Trichia plebeia* (Draparnaud). *Perforatella* (Fig. 2) can be readily distinguished from *Trichia* by its single large dart sac (Hudec 1963). This can be easily recognised in all but the smallest juveniles, and in mature individuals the distinctive chitinous dart (pl. 16, Fig. 1) can be clearly seen. There are two pairs of mucus glands and the flagellum and epiphallus are long and thin; the spermatheca is also distinguishable from the bulbous form found in *Trichia*, being a finger-like widening of the spermatheca duct.

*Trichia*, *Ponentina* and *Perforatella* are placed in the subfamily Hygromiinae but some members of the Monachinae may also be confused with these snails. Juveniles of *Monacha cantiana* (Montagu) possess periostracal hairs but the rapidly expanding whorls and large aperture are clearly distinct from *Trichia*. With the smaller *Ashfordia granulata* (Alder), however, periostracal hairs are retained in the adult (pl. 16, Fig. 2) and, although distinctive to anyone familiar with them, they are often confused with *Trichia*, which may partly account for the few Continental records of this species (Bishop 1976). The absence of both dart sacs and mucus glands (Fig. 3), with the flagellum a mere stump, allows their discrimination.

<sup>1</sup> Whilst it is convenient to continue to use the name *rubiginosa*, it should be noted that *Helix rubiginosa* Schmidt 1853 is a junior primary homonym of *Helix rubiginosa* Gould 1848 and will need to be replaced.



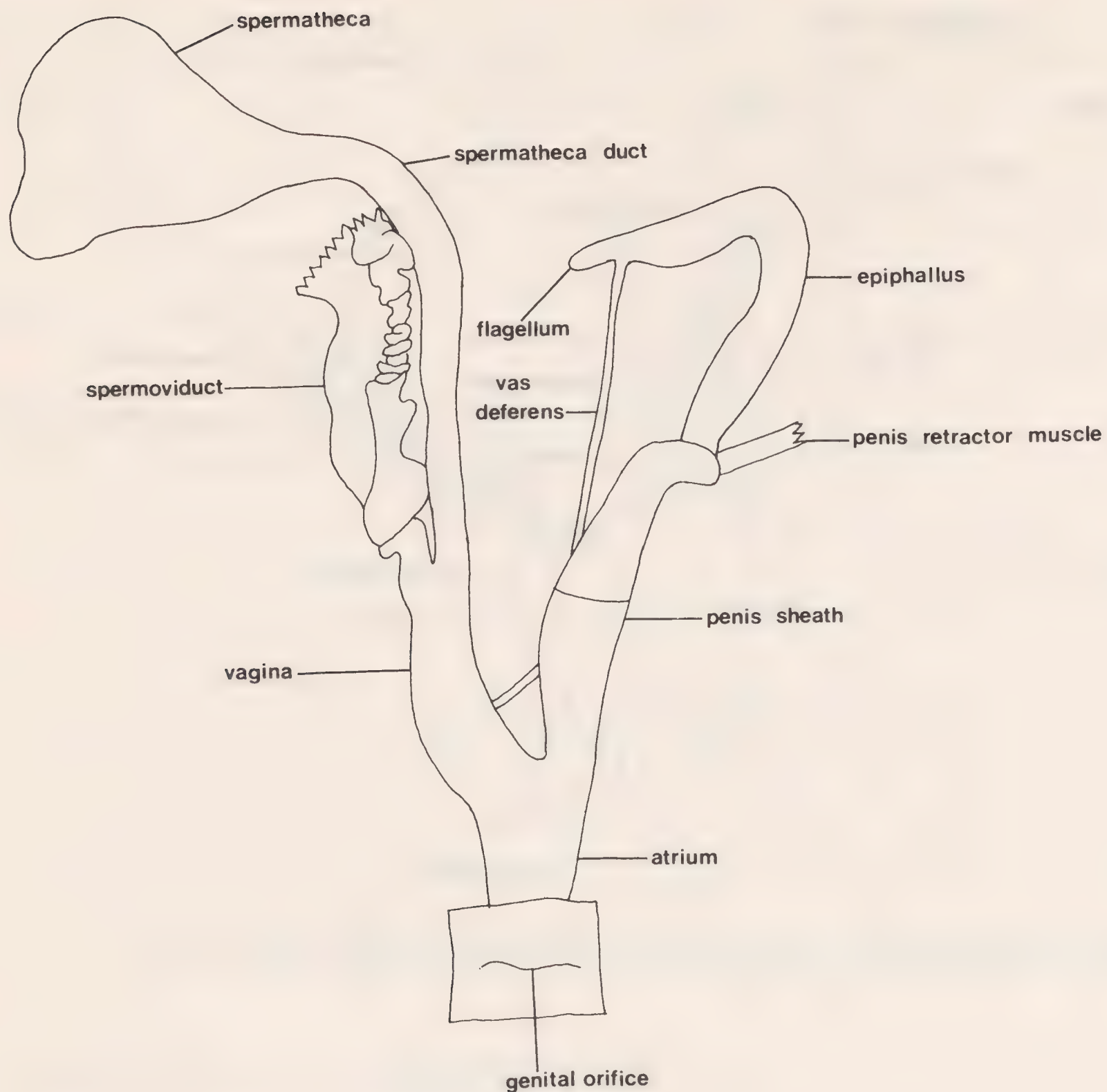


Fig. 3. *Ashfordia granulata* genitalia. Specimen from Box Hill, Surrey, February, 1983.

#### SHELL CHARACTERS

Although shells of these different snails might provide unsatisfactory criteria for characterising genera, shells are of value for discriminating at lower taxonomic levels. For example, mature *Perforatella rubiginosa* do not form an internal rib at the aperture as does *Trichia* and, when closely examined, the numerous long hairs found on *Ashfordia granulata* cannot be confused with the thicker hairs of *Perforatella rubiginosa* and *Trichia* which, though variable, are more often curved than those of *Ashfordia granulata*.

#### THE BRITISH RECORDS OF *PERFORATELLA*

So far the following are the recorded localities for *Perforatella rubiginosa* in Britain: Syon Park, Middlesex (National Grid reference: TQ 176766); South Stoke, Oxfordshire (SU 5983); Pangbourne, Berkshire (SU 6277) (= *Hygromia liberta* (Westerlund) *sensu* Quick 1960); Aylesford, Kent (TQ 7358). The record of a fossil specimen from the Icenian Crag of Southwold (Kennard & Woodward 1899, Harmer 1914, Ellis 1926, Verdcourt 1982) must be



discounted as, after this specimen (BM(NH) G.2176) was cleaned ultrasonically, a distinct apertural rib could be seen.

These British populations of *Perforatella rubiginosa* are amphibious, being found in muddy riverside fields. The population I sampled at South Stoke was evidently in a habitat too wet for *Trichia hispida* which, although occurring close by, was not found mixed with *Perforatella*. Specimens from South Stoke were smaller than the Syon Park specimens and free of the heavy encrustation of debris found on these shells. This absence of debris may be associated with their distinctive microsculpture (pl. 16, Fig. 3). Such microsculpture reduces the effective contact surface area of the shell (Solem 1976) but hairs alone are clearly not preventing such accumulations on the Syon Park specimens (pl. 16, Fig. 4). The particles are firmly held with what may be dried mucus from the snail; in fact, the coating is extremely difficult to remove with the shells disintegrating in an ultrasonic cleaner before becoming fully clean.

The South Stoke specimens complete their annual life cycle in a different phase to the Syon Park population. After overwintering as fully grown specimens in which the reproductive organs are not completely formed, sexual maturity is reached in late February and early March. The Syon Park specimens are mature in June and overwinter as juveniles.

When the Continental populations of *Perforatella rubiginosa* are examined they occupy different habitats. For example, the stenoecious habit of populations from Belgium is exclusively freshwater intertidal (Vader 1977) whereas records from eastern Europe cover a wide range of habitats including woodland but these populations may include more than a single euryoecious species.

#### THE SPECIES GROUPS

The real difficulty, therefore, is not the discrimination of genera but the status of forms within both the *Trichia hispida* and the *Trichia striolata* groups, and forms within *Perforatella rubiginosa*. Critical evidence would come from detailed mapping of the various forms as indicated by Verdcourt (1982) but there are a number of problems in understanding what forms are involved before detailed consideration can be given to their distribution and status. For example, the significance of different microsculpture on populations of *Perforatella rubiginosa* has not been fully investigated and an objective basis for analysing variation in *Trichia* requires further development (Naggs 1982). Once a stronger foundation for identifying morphological groups is established, the taxonomic status they might be afforded could very much depend on the species concept adopted. Some of the difficulties will be examined in a forthcoming publication.

#### ACKNOWLEDGEMENTS

I wish to thank Dr. M. P. Kerney for making the census records of the Conchological Society available and for providing helpful comments; Dr. B. Verdcourt for providing material from Syon Park; Mr. J. Bebbington for loaning material from the Quick collection at Juniper Hall Field Studies Centre. I am also grateful to Miss A. Thomson for producing the scanning electron micrographs and to Dr. P. B. Mordant for helpful comments.



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# MOLLUSCAN ZONATION ON ROCKY SHORES IN MALTA

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(Accepted for publication 18 December 1982)

*Abstract:* A Quantitative zonation study of intertidal molluscs in Malta shows that the Lewis (1964) zonation scheme is applicable to the microtidal coasts of the Mediterranean. The monotonous limestone substrates highlight the effects of wave action and exposure on molluscan distribution. Comparison with sublittoral transects reveals a distinct break between the intertidal and sublittoral fauna on the island. Although Malta has a small species pool, species richness at individual sites is high compared to other areas of the Mediterranean. Substrate type is suggested as a major control of species richness.

## INTRODUCTION

Comparison of shores around the world has shown that similar kinds of organisms tend to occur in broadly similar positions or zones upon the shore (Stephenson and Stephenson 1949, Southward 1958, Lewis 1964). However, the detailed distributions of organisms within these universal zones is often only poorly known. Moreover, when compared to the macrotidal shores of northern Europe (Lewis 1964) there is surprisingly little quantitative data on the distribution of intertidal molluscs in the Mediterranean, where most quantitative studies have been confined to the sublittoral zone.

Intertidal animals are vulnerable to the effects of pollution and human disturbance. In view of the present concern over the degradation of the Mediterranean marine environment (Walgate 1980) baseline studies of the littoral and shallow sublittoral zones are desirable. Intertidal molluscs are usually abundant, easy to sample and generally readily identifiable and are thus potentially good environmental indicators.

This study describes the quantitative distribution of intertidal molluscs around the island of Malta, for which there are extensive quantitative data available for the molluscs of the sublittoral zone (Wilkinson *et al.* 1967).

Despite the large number of qualitative molluscan studies made on the nearby coasts of Tunisia and Sicily, Malta has received little attention. Early qualitative studies in the islands (e.g. Caruana 1867) consisted of little more than annotated species lists. Distribution data were later supplied by Despott (1918) for Marsaxlokk Bay, and Gatto & Despott (1919) attempted to assemble data for the whole island. More recently, detailed quantitative studies of the sublittoral fauna have been made by Biggs & Wilkinson (1966) and Wilkinson *et al.* (1967). Data were collected from a total of six submarine transects at Weid-iz-Zurrieq, Paradise Bay and Delimara Point. Sampling between 1 m and 5 m was conducted at 1 m intervals, thus providing good coverage of the shallow sublittoral zone.

The work of local naturalists has provided species lists for many locations on the island (Cachia 1973, 1975) and studies of individual species or genera (e.g. *Lithophaga lithophaga*, Aguis 1976). A number of physiological studies related to the zonation of common intertidal species such as *Patella caerulea* and *Monodonta turbinata* have also been conducted at the University of Malta (Bannister *et al.* 1966).

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*Wave action and exposure*

The assessment of exposure is largely a subjective exercise, but some use can be made of the relationship of wave action to wind strength and direction and to offshore topography. The predominant winds in Malta are northeasterly to northwesterly, and they expose most of the northern and eastern coasts of the island to high waves particularly in winter. The northwesterly Sirocco winds have been known to produce waves of up to 6 m (Admiralty 1963). On the western and southern coasts, submarine cliffs tend to increase the effects of swell and wave impact on the shore. Thus there are few striking differences in potential exposure between different areas of the island, and local shoreline configuration tends to be the most important control of exposure.

*Tides*

Even by Mediterranean standards the tidal range of Malta is low, with a maximum spring range of 0.15 m at Valletta (Admiralty 1963). There is very little variation in this figure around the island, although the presence of extensive littoral platforms at some sites tends to produce a large change in emersion with a small change in tidal level.

Owing to the small tidal range, meteorological variations in sea level are often far more important than tidal ones. For example, during the spring low atmospheric pressure may cause a drop of up to 0.5 m in Mean Sea Level (MSL).

*Climate*

Malta has a typical Mediterranean climate, with hot dry summers and warm wet winters. Freezing temperatures have not been recorded in the islands, and the maximum temperature is 39°C. Thus temperature stress is unlikely to have a great influence on the zonation pattern. Of the mean annual rainfall of 609 mm, two-thirds falls between October and January, but it is evenly distributed between these months.

*Substrate*

The Maltese littoral is characterised by very uniform Tertiary limestones (Pedley *et al.* 1976). Substrate type can therefore be discounted as a source of local variation, although weathering of the limestone produces distinctive littoral morphologies which may influence zonation (Paskoff and Sanlaville 1978).

*Water temperature and salinity*

Mean water temperatures around Malta vary from 14°C in February to 26°C in August (Admiralty 1963) and it is unlikely that lethal temperatures are attained for any species. Conductivity meter measurements of the salinity of water samples collected at MSL at 8 sites around the island gave figures of 38‰–39‰, indicating very little variation over the island as a whole. This is largely because of the lack of fresh water outlets on the island.



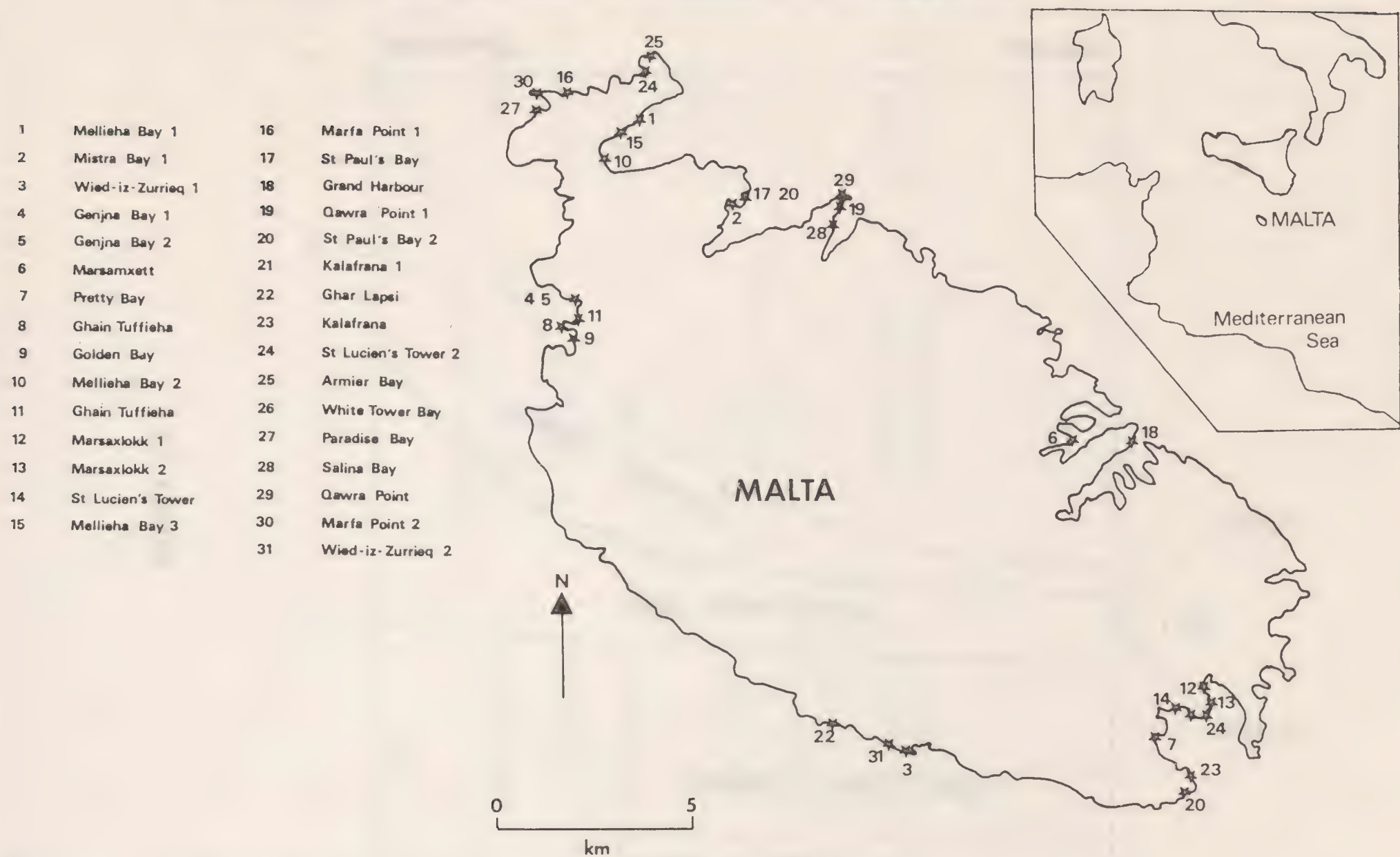


Fig. 1. Map of Malta showing localities mentioned in the text.

### METHODS

Quantitative samples of the molluscan fauna from the littoral and shallow sublittoral zones were collected in September 1980. Over thirty sites were sampled on rocky shores, as were most of the sandy bays on the island, although these yielded no living fauna. The rocky shore sites seem to represent a fair sample of the exposure conditions and morphology types on the island, although problems of access dictated their spatial distribution (Fig. 1).

The fauna was sampled by taking quadrats at vertical intervals of 0.25 m or 0.50 m, depending on transect length, relative heights being calculated using a graduated staff and abney level. As it was impractical to level in each transect to a benchmark, tidal datum was established by taking measurements of high and low tide, which were then corrected using Admiralty tide tables (Admiralty 1979). Quadrat size was normally 0.25 m<sup>2</sup> or 0.5 m<sup>2</sup>, with 0.01 m<sup>2</sup> quadrats being used to subsample dense populations. The data were later standardised to individuals/m<sup>2</sup> for comparability. All the material was identified using the collections of the British Museum (Natural History). Taxonomic authorities are shown in the species list.

### RESULTS AND DISCUSSION

The zonation scheme (Fig. 2) was drawn up according to the terminology of Lewis (1964). In addition, Table 1 shows the dominant species of each zone for different exposure conditions, also classified according to Lewis (1964). The dominant species were defined on the basis of their density expressed as individuals/m<sup>2</sup>. Although most individuals of each species will be restricted to their assigned zone, in certain circumstances some may stray beyond the limits of that zone.

Consideration of the zonation pattern shows that the zones described by Lewis (1964) are all recognisable in the Maltese littoral. As might be expected, the composition of the fauna and the extent of each zone vary with exposure. In sheltered conditions the littoral fringe is



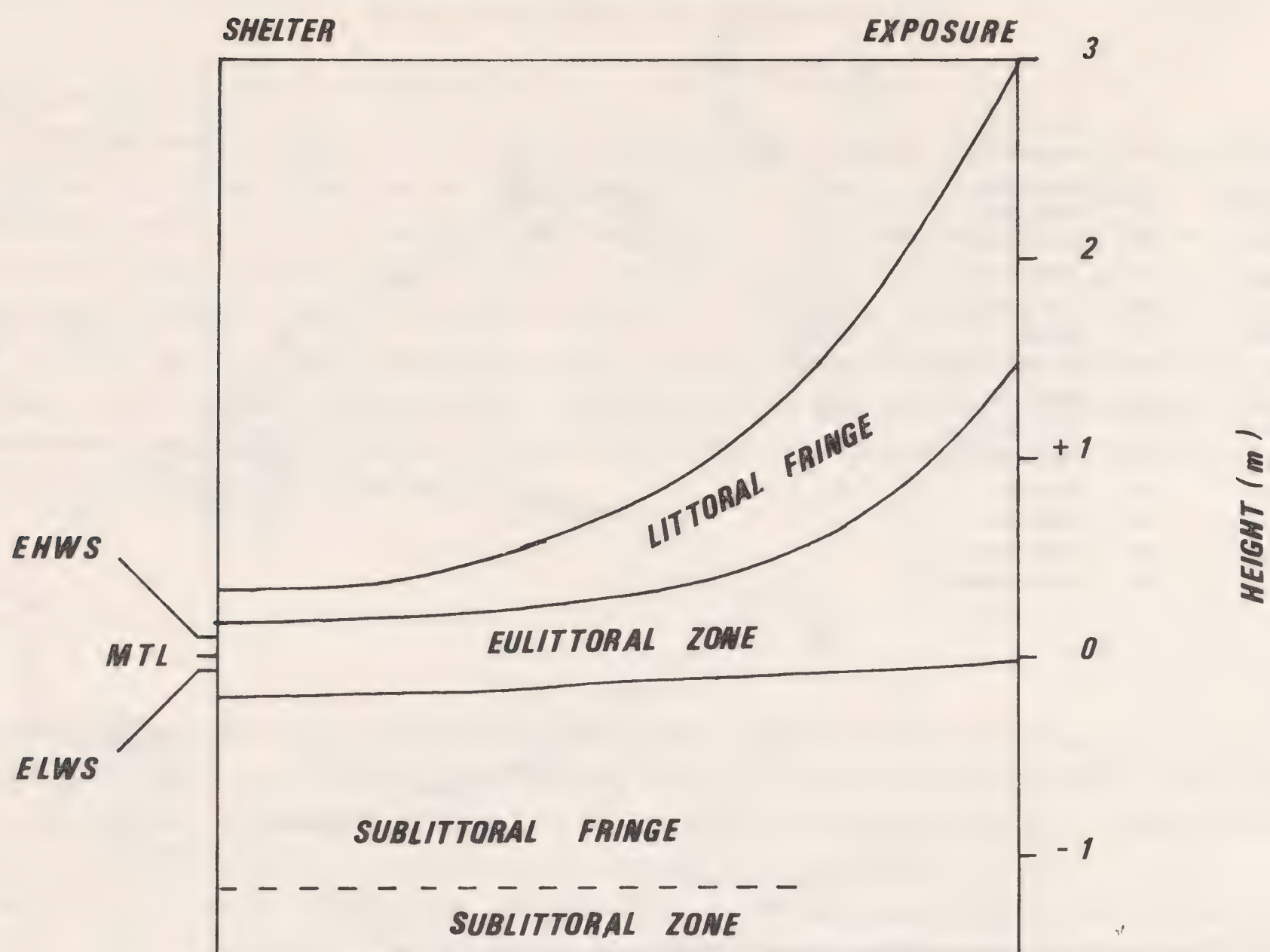


Fig. 2. Zonation scheme for rocky shores in Malta, after the terminology of Lewis (1964).

very narrow, extending less than 1 m above MTL (mean tidal level). In exposed conditions, however, the littoral fringe may expand to 3 m or more above MTL, while the eulittoral zone similarly increases to a width of 1.5 m. Unlike the macrotidal coasts studied by Lewis (1964), the limit of the eulittoral, defined by the upper limit of barnacles, extends well above EHWS, which reaches a maximum height of only +0.10 m in Malta. On sheltered coasts, there may be a sublittoral fringe characterised by the presence of the gastropods *Cerithium rupestre* and *Ocenebrina edwardsi*. The fact that these species are restricted to the upper 1 m of the sublittoral (Biggs and Wilkinson 1966, Wilkinson *et al.* 1967) would seem to suggest that this division is justified. On more exposed coasts, *Cerithium rupestre* is replaced by *C. vulgatum* and *Columbella rustica*, which by extending well into the sublittoral indicate the loss of any identifiable fringe under exposed conditions.

This scheme largely confirms the limited observations on the relative zonal positions of some species made by previous workers. For example, the zonal positions of *Gibbula divaricata* (upper sublittoral to lower eulittoral) and *Monodonta turbinata* (mid-eulittoral) confirm the supposition of Micallef and Bannister (1967) that the latter is exposed to aerial conditions more frequently.

While the general features of the scheme provide a rough description of the conditions at each site, they also hide many important variations that occur because of different substrates and littoral profiles. In general, the various types of rocky shores can be grouped into cliffs, platforms and boulder shores. The following section considers each of these in turn, as well as the different types of pools found in the latter two habitats.



TABLE 1  
Dominant species on rocky shores in Malta

Zone	Very sheltered	Sheltered	Semi-exposed	Exposure conditions	Very exposed
Littoral Fringe	<i>L. neritoides</i>	<i>L. neritoides</i>	<i>L. neritoides</i>	Exposed	<i>L. neritoides</i>
	<i>Patella caerulea</i>	<i>P. caerulea</i>	<i>P. lusitanica</i>	<i>P. lusitanica</i>	( <i>Chthamalus stellatus</i> ) <i>P. lusitanica</i> <i>P. caerulea</i>
				<i>P. caerulea</i> <i>Monodonta turbinata</i> <i>V. triqueter</i>	<i>V. triqueter</i>
Eulittoral zone					
Sublittoral Fringe					



*Rocky shore habitats*

The cliffs around Malta result from the Tertiary tectonic uplift of the northern and western coasts of the island, and are largely restricted to these areas. The cliffs are often very steep and drop almost vertically to the sea bed. Consequently, they are normally subject to exposed conditions.

A typical cliff transect is that from Weid-iz-Zurrieq (Fig. 3), which is also close to some sublittoral transects described by Biggs and Wilkinson (1966) and Wilkinson *et al.* (1967). This exposed site is composed of Lower Coralline limestone, and apart from a narrow platform at about MTL, the cliff drops vertically to the seabed 40 m below (Wilkinson *et al.* 1967). The exposed conditions are reflected in the extent of the littoral fringe, with dense populations of *Littorina neritoides* present up to +3 m. *L. neritoides* reaches its maximum density of 3,000/m<sup>2</sup> at about 1.5 m. Below this level it rapidly thins out to be replaced by the barnacle *Chthamalus stellatus*, which dominates the top of the eulittoral zone at similar high densities. The main part of the eulittoral zone is subdivided between the limpets *Patella lusitanica* and *P. caerulea*, and the vermetid gastropod *Vermetus triqueter*. *Patella lusitanica* is usually found zoned above *P. caerulea* on exposed shores, and in this case the greatest densities of *P. lusitanica* are found slightly above those of *P. caerulea*, although the two populations overlap to some extent. At other sites this division is more distinct, although the general increase in elevation with exposure exhibited by *P. caerulea* means that some isolated individuals will be found with *P. lusitanica*.

The base of the eulittoral is dominated by a thick encrustation of *Vermetus triqueter*, which extends for 0.05 m either side of MTL. These vermetids form a gregarious mass at densities of up to 3,600/m<sup>2</sup> to the almost total exclusion of other species. Isolated individuals may be found at elevations of up to +0.40 m on this and other exposed sites, but the highest concentrations are always found within 0.1 m of MTL. They are most common at exposed sites, usually on small platforms which trap water at high tide, but they are also present at lower densities on more sheltered, less inclined substrates.

The lower part of the eulittoral also contains a few *Mytilus galloprovincialis* and *Chiton olivaceus*, both of which may be found at greater densities at other exposed sites. The base of the eulittoral is clearly defined just below MTL by the lower limit of *Patella caerulea* and *Vermetus triqueter*.

There is no evidence for the existence of a sublittoral fringe at this or any other exposed site, and typical sublittoral species extend to within a few centimetres of MTL. The upper 1 m of the sublittoral zone contains the gastropods *Conus ventricosus*, *Columbella rustica*, *Pisania maculosa*, *Fasciolaria lignaria* and *Thais haemastoma*, all except the last having been recorded at greater depth at this site (Wilkinson *et al.* 1967). The presence of these species is probably facilitated by the thick growth of the alga *Cystoseira* on the small platform just below MTL. It is noticeable that these species predominantly have sturdy shells and a relatively large foot in comparison to shell size, which may well help them withstand considerable wave impact. Increased wave stress may account for the lack of species with tall or fragile shells, such as *Cerithium rupestre* or *Rissoa variabilis*, which are common in the sublittoral fringe of more sheltered sites. *R. variabilis* is also found at greater depth at this site according to Wilkinson *et al.* (1967).

Relatively extensive platforms at or near MTL are found in many parts of Malta and in all types of exposure. They are normally produced by marine erosion of the limestone substrate, particularly along horizontal fractures (Paskoff & Sanlaville 1978). Where these platforms are subject to direct wave action, they are often broken into a series of pools or potholes the fauna of which is dealt with separately.

The exposed platform at Kalafrana (Fig. 4) demonstrates many of the salient points of platform zonation. The platform here is composed of gently inclined Lower Globigerina



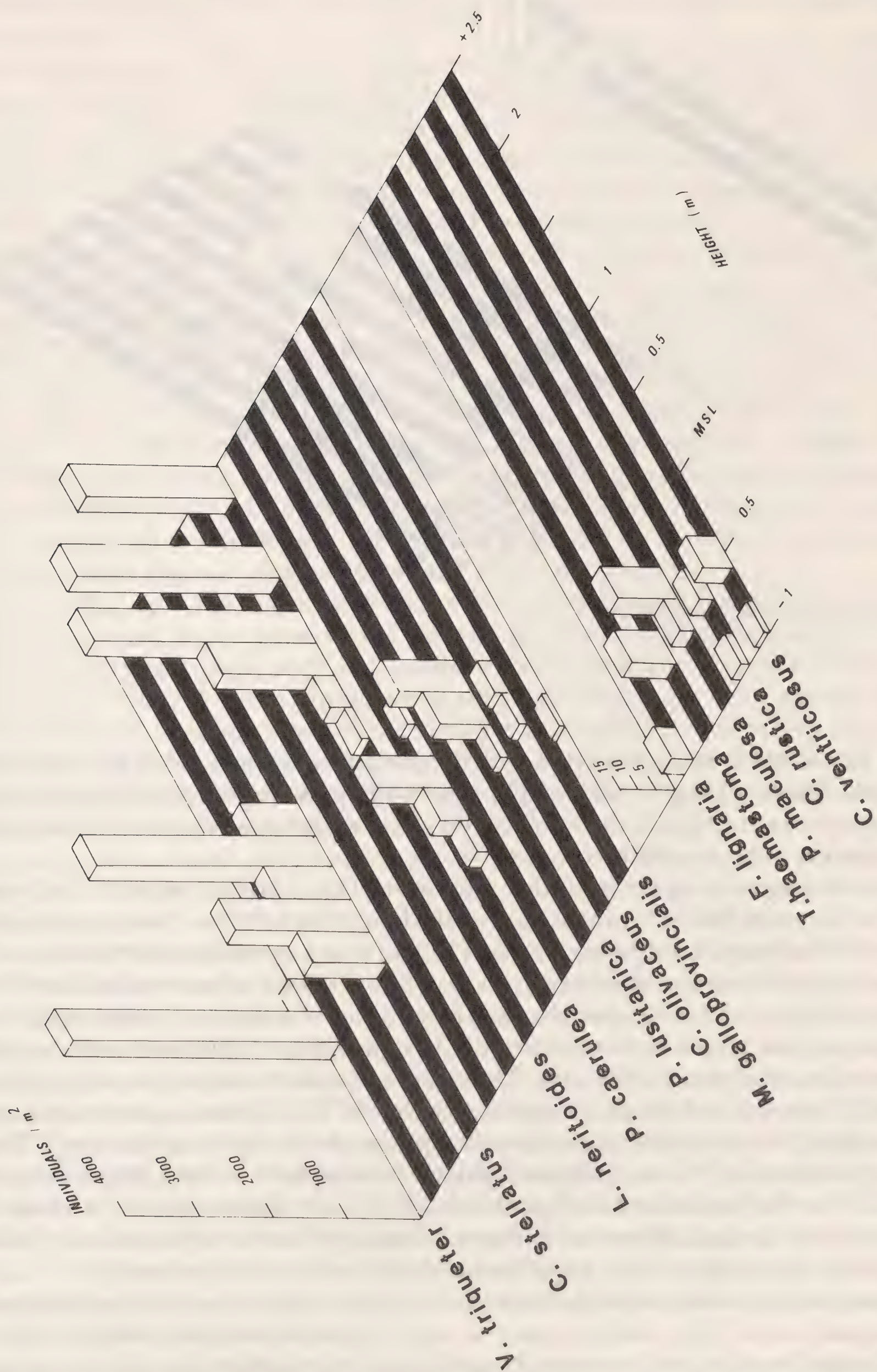


Fig. 3. Rocky shore zonation at Weid-iz-Zurrieq. A sublittoral transect for this site is shown in Fig. 7.



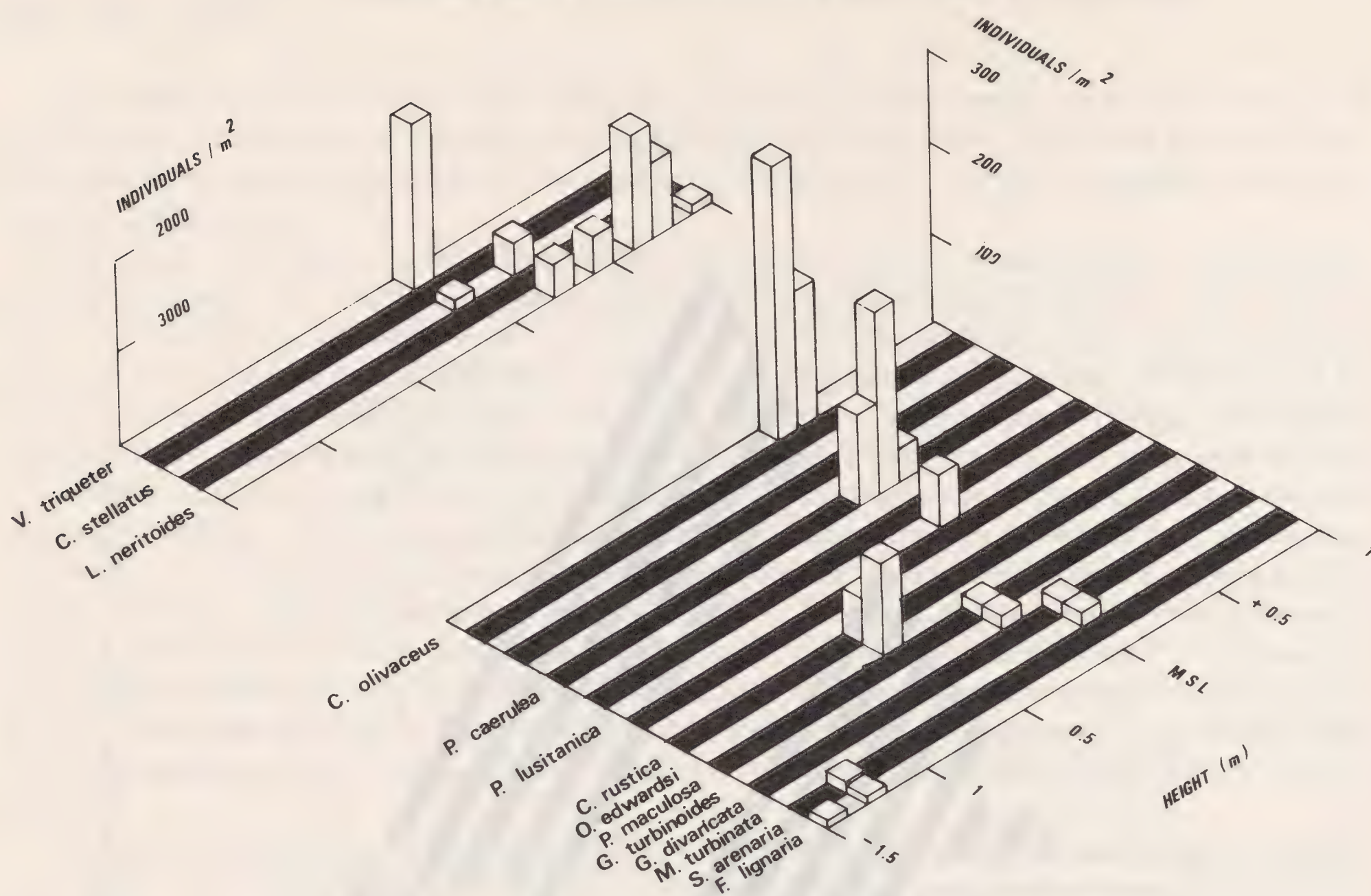


Fig. 4. Rocky shore zonation at Kalafrana.

Limestone. Below MTL this is carpeted with dense *Cystoseira*, and broken by a series of deep clefts along the bedding planes. Above MTL the bedding planes are picked out by erosion to provide a highly crenulated substrate. Where the platform is backed by vertical rock, the base normally contains a deep crevice.

The littoral fringe is again occupied exclusively by *Littorina neritoides*, although the maximum density of 2,000/m<sup>2</sup> is rather low, with figures of 5,000/m<sup>2</sup> having been recorded from other platform sites (e.g. Qawra Point). The fact that *L. neritoides* only extends to +1.5 m at Kalafrana may reflect the absence of the combined effects of wave splash and swell at comparable cliff sites, which have no seaward projections to dissipate the force of the waves.

The upper eulittoral zone is characterised by the presence of *Chthamalus stellatus*, although again at lower densities than at cliff sites. The same is true of the mid-eulittoral species *Patella lusitanica* and *P. caerulea*, and they also appear closer to MTL. *Chiton olivaceus* is also numerous in this zone, aided by its ability to occupy the tiny potholes found in this area. The lower eulittoral is dominated by *Vermetus triqueter*, which occurs at densities of 2,000/m<sup>2</sup> at or slightly below MTL. The horizontal crevices at this level provide shelter for the trochids *Gibbula divaricata*, *G. turbinoides* and *Monodonta turbinata*. Although these localised concentrations are relatively dense, they make only a small contribution to the total biomass.

The *Cystoseira* mat, which extends from about -0.15 m to -1 m, is largely devoid of its usual gastropod fauna. The platform here is highly agitated by wave action, which must make it difficult for associated gastropods such as *Rissoa variabilis* and *Bittium reticulatum* to maintain a foothold on the algal fronds. Instead, some bare areas of rock are inhabited by individual *Vermetus triqueter*, although at far lower densities than are found in the gregarious concentrations at MTL. Only in small potholes can motile gastropods such as *Ocenebrina*



*edwardsi* be found. Below the *Cystoseira*, at about  $-1$  m, all available crevices are occupied by the sea-urchin *Sphaerechinus granularis*, and in common with other sites where this species is present, the hollows are often shared by the gastropods *Fasciolaria lignaria* and *Columbella rustica*. These species may thus gain some protection from predators which are dissuaded by the sea-urchins' spines. Also at this level the large vermetid *Serpulorbis arenaria* is present at densities of up to  $10/\text{m}^2$ .

More sheltered platform sites exhibit noticeable differences, particularly in the extent of the littoral fringe and the composition of the sublittoral fauna. Pretty Bay, about 1500 m to the northwest of Kalafrana, has a similarly gently inclined substrate, with numerous pools near MTL. The upper part of the platforms is above the reach of most waves, and the shore descends below MTL in a series of small ledges and pools to an extensive platform at  $-0.75$  m, which in some places extends as much as 10 m from the shore.

The littoral fringe here does not extend beyond  $+0.50$  m, although the densities of *Littorina neritoides* may reach  $4,500/\text{m}^2$ . The whole zone is compressed into the area between  $+0.50$  m and  $+0.30$  m, as *L. neritoides* is replaced by a dense belt of *Chthamalus stellatus* below this level. The barnacles are in turn replaced by *Patella caerulea* and *Chiton olivaceus* at  $+0.20$  m, *Patella lusitanica* being largely absent from sheltered shores. Numerous small crevices again promote high densities of *Chiton olivaceus*, with up to  $500/\text{m}^2$ . The lower eulittoral is dominated by *Vermetus triqueter*, although the highest concentration occurs at  $-0.05$  m, slightly lower than on exposed sites. *V. triqueter* is not found at the other sheltered sites, and here it is probably present by virtue of the water retaining properties of the stepped littoral profile. On other sheltered shores, the position occupied by *V. triqueter* is taken by *Gibbula divaricata* or *Chiton olivaceus*, depending on the substrate type.

At Pretty Bay, as at other sheltered sites, a distinct sublittoral fringe is present (see Fig. 5). This is characterised by the presence of *Cerithium rupestre* and *Ocenebrina edwardsi* in association with other small gastropods, such as *Columbella rustica*, which are not restricted to this zone. The extensive sublittoral platform provides abundant shelter for these species in numerous crevices. However, the algal cover of the platform is dominated by *Padina pavonia*, the small, flexible, cup-shaped fronds of which are largely devoid of gastropod fauna. This might explain the slightly lower densities of *Cerithium rupestre* in comparison with sites where the algae *Cystoseira* or *Halopteris* are dominant.

A number of limestone platforms which are backed by cliffs are covered with boulders of various sizes. The effect of the boulders is to break the littoral zone into a series of pools and small platforms, and to reduce the effects of exposure close to the shore. This produces a modification of the zonation pattern, which is most marked on exposed shores.

The boulder shore at Paradise Bay (Fig. 6) is typical of most exposed boulder shores. The transect taken here covers about 15 m of boulders and pools, thus covering the entire range of wave attenuation from the highly exposed seaward boulders to the sheltered pools at the landward end. At the seaward end of the transect, the vertical face of a prominent boulder is covered by *Patella caerulea*, while crevices in the rock are inhabited by large *Monodonta turbinata*. The boulder behind this forms a horizontal platform dominated by *Vermetus triqueter* and *Patella caerulea*, while *Chiton olivaceus* occurs in crevices at the back of the platform.

In the lee of these two large boulders is a sheltered pool connected directly to the sea and itself filled with smaller rocks. The fauna here is composed mainly of the trochids *Gibbula divaricata*, *G. turbinoides* and *G. varia*, along with hermit crabs occupying the shells of species usually found in more exposed locations. *G. divaricata* is found in particularly high densities under small boulders in this pool.

At the steeply inclined landward end of the transect, the trochids are replaced by *Patella caerulea*, although at much lower densities than in the exposed section of the transect. Because of the lower level of exposure vermetids are absent from this area, and their normal position at about MTL is occupied by *P. caerulea* and barnacles. The lower exposure also means that



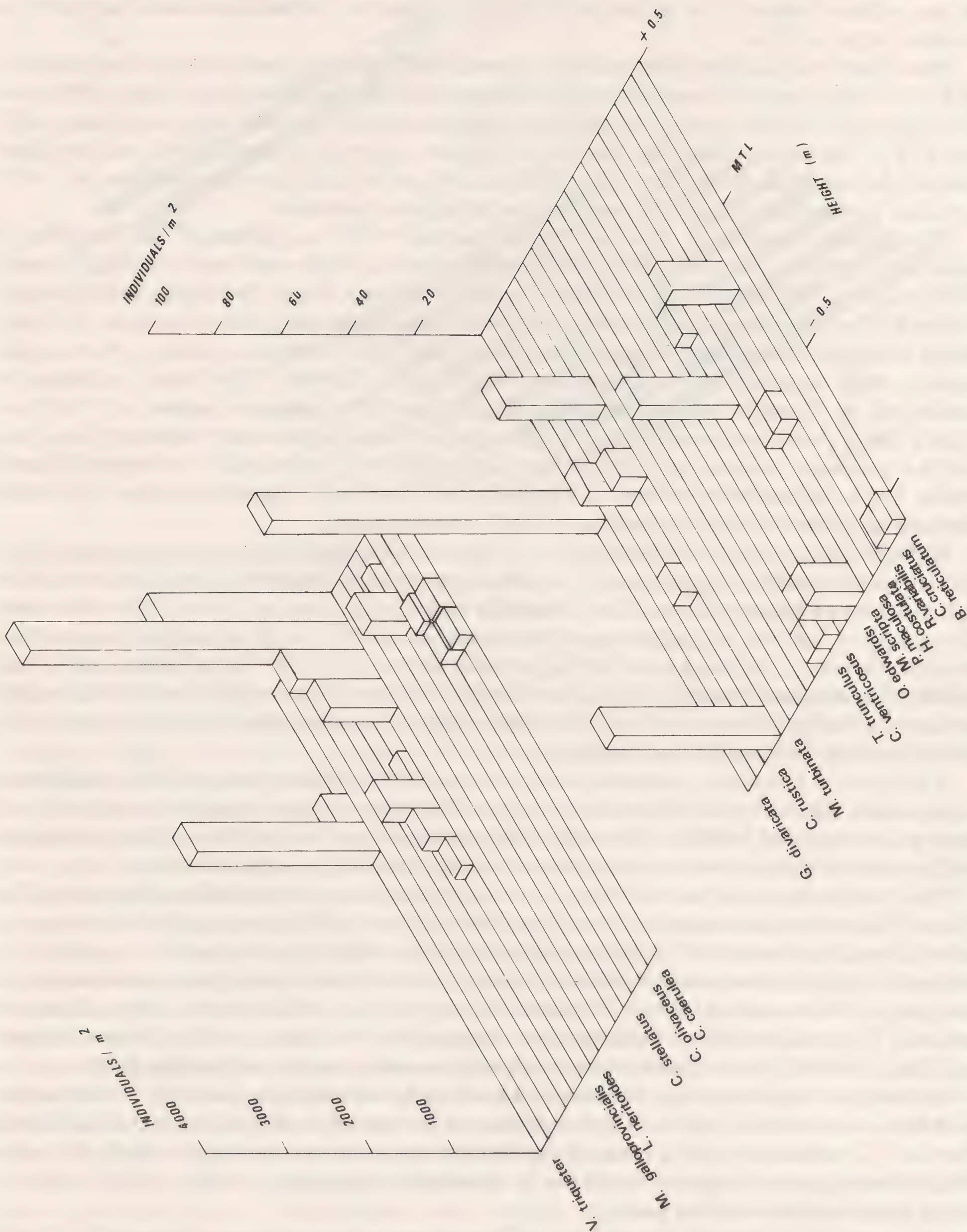


Fig. 5. Rocky shore zonation at Pretty Bay.



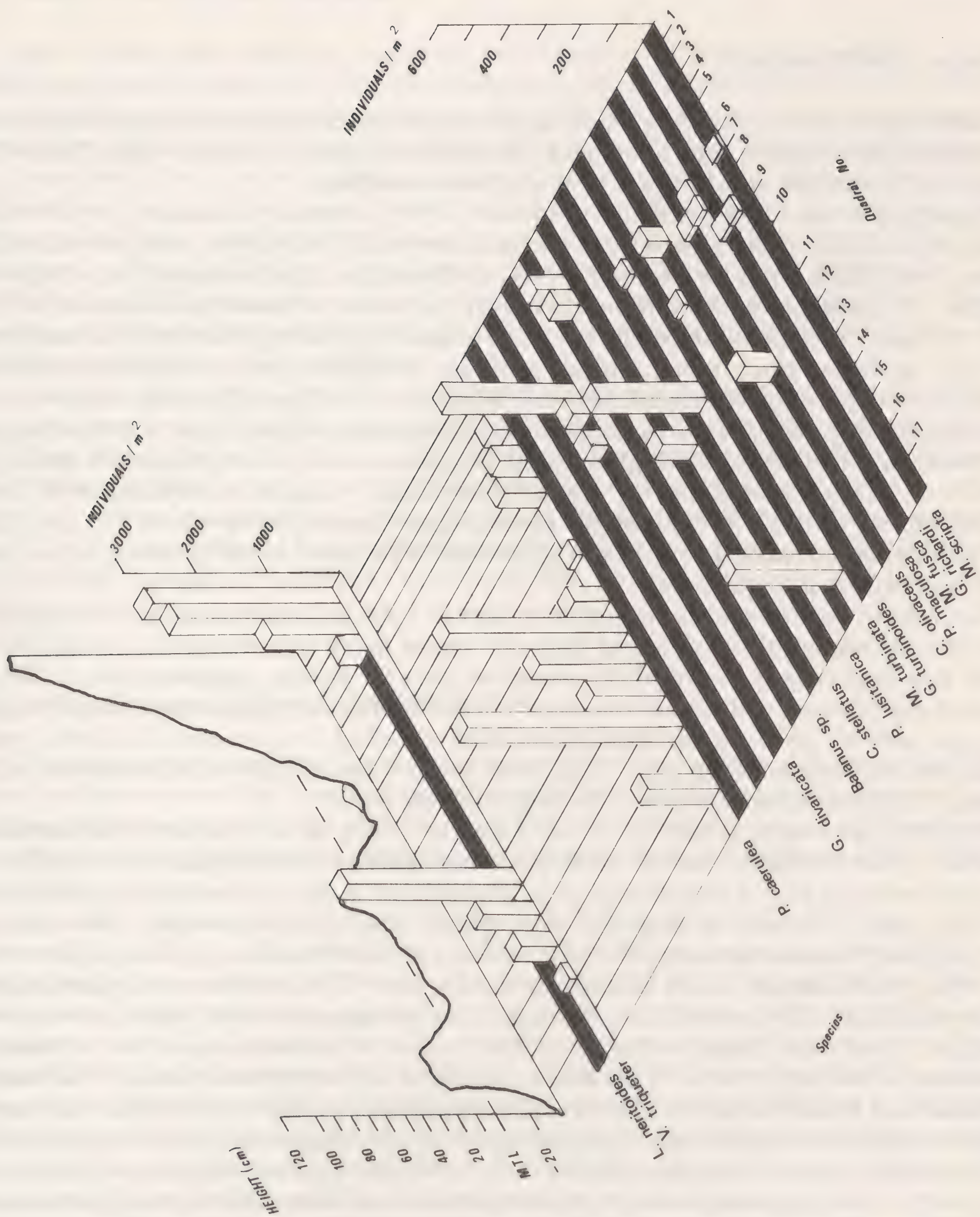


Fig. 6. Rocky shore zonation at Paradise Bay.



*Littorina neritoides* reaches down to MTL, almost completely replacing the barnacles above this level.

Thus the relationship between zonation and tidal level on this shore is far from simple, and such sites may exhibit features of both exposed and sheltered shores in the confines of a few metres.

### *The fauna of special habitats*

On all types of shore, there are recurring discrete habitats which bear little relation to the general zonation scheme, and sometimes have zonation patterns of their own. Those that occur most frequently on Malta are pool and crevice habitats.

According to the classification of Levander (1900), the most common types of littoral pools are sub-saline pools, splash pools and seawater pools. Sub-saline pools are most often found at very high levels on exposed shores, and contain high concentrations of *Littorina neritoides*. Occasionally they occur on more sheltered shores at lower elevations and with a lower biomass. Such pools are subject to wave splash only during winter storms, and some may dry up during the summer. Splash pools are found at up to +3 m on very exposed platforms, and are subject to more frequent inundation. At Qawra Point the fauna of such pools consists of *L. neritoides* (up to 4,500/m<sup>2</sup>) and *Chthamalus stellatus* (up to 10,000/m<sup>2</sup> in pool overflows). At Marfa Point, the highest splash pool has a similar fauna, whereas a small pool at +0.5 m, subject to considerably greater wave splash, supports a population of *Patella caerulea* (102/m<sup>2</sup>) some 0.10 m above the general upper limit of the species at this site. Thus both sub-saline and splash pools seem to allow some of the upper shore species to extend their range and density at high levels.

In contrast, seawater pools are subject to almost constant inundation, and consequently often have a comparatively rich and distinctly zoned fauna. For example, a small pool at Pretty Bay located just above MTL contained over 60 *Mytilus galloprovincialis*, 9 *Gibbula divaricata* and 3 hermit crabs in an area of 0.2 m<sup>2</sup>. The *Mytilus* were grouped around the edge of the pool, with *G. divaricata* sheltering about 0.05 m below the rim, and the hermit crabs grouped at the bottom of the pool. Thus there seems to be a zonation reflecting decreased exposure conditions from the top to the bottom of the pool.

The Maltese littoral is rich in crevice habitats, owing to the erosion of the limestone substrate. Most frequently they occur as horizontal fractures at or slightly above MTL. For example, at Salina Bay, a narrow crevice (c. 50 mm high) is cut into the back of a platform at +0.10 m, and is subject to frequent wave splash. This crevice contains *Chiton olivaceus* (200/m<sup>2</sup>) and *Monodonta turbinata* (150/m<sup>2</sup>), both of which are found on the roof of the crevice, and a few *Patella caerulea*, which inhabit the crevice floor. The first two species are found at greater densities in the crevice than on the open rock, perhaps because of the greater degree of protection from wave impact afforded by the crevice. A similar pattern can be found at Kalafrana, where a crevice at + 50 mm is inhabited by the trochids *Gibbula divaricata*, *G. turbinoides* and *Monodonta turbinata*, all of which are absent from open rock surfaces during the day. Presumably these motile gastropods forage from this refuge at night or during high tide.

Vertical crevices are less common, but they do provide scope for certain eulittoral species to extend their normal zonal limits in the damp shaded conditions of crevices. On the eastern side of Qawra Point, a crevice extending from below MTL to +0.50 m supports a dense population of large *Monodonta turbinata* up to a height of +0.30 m, which is 0.10 m higher than the limit of this species on the open rock.

Mention should also be made here of the major endolithic species which inhabits the limestone substrate, namely the date-mussel *Lithophaga lithophaga*. This species is widely distributed (Agius 1976), and its burrows may be found in dense concentrations between



MTL and  $-0.50$  m in all exposure conditions. Calculating the actual density of this species is difficult, however, as many disused burrows are inhabited by other species such as *Barbatia barbata*.

### *Relationships between molluscs and algae*

Algal fronds and holdfasts constitute an important habitat for many of the small gastropod species found in the shallow sublittoral. Often, recurring associations of certain species with particular types of algae were evident. *Cystoseira* algae were the most common in the sublittoral fringe, usually forming a dense cover (up to 90% surface coverage) from  $-0.10$  m downwards. The holdfasts often contained *Cerithium rupestre* at sheltered sites, whereas *Columbella rustica* and *Pisania maculosa* were more frequent occupants at exposed sites. *Bittium reticulatum* was often found in the fronds, an association noted by Wilkinson *et al.* (1967) in the sublittoral at Weid-iz-Zurrieq. These associations are also similar to those found in Corsica by Molinier (1960), who recognised a *Cystoseira crinata* biocoenosis associated with *Cerithium rupestre* and *Bittium reticulatum* at sheltered sites, and a *Cystoseira stricta* biocoenosis associated with *Vermetus triqueter* at exposed sites.

At some sheltered sites, however, the *Cystoseira* mat may be replaced by either *Halopteris* sp. or *Padina pavonia*. The former may form a dense band just below the eulittoral zone, and was often found to contain large populations of *Cerithium rupestre*, especially in Marsaxlokk Bay. *Padina pavonia* was particularly prevalent on platform shores between  $-0.15$  m and  $-1.5$  m, but it was rarely associated with a particular species, the flat open fronds apparently providing a poor gastropod habitat. Dense stands of *Posidonia oceanica* were found below 1 m on the sandy bottoms of Marsaxlokk and Mistra Bay, but little fauna was found on the edges of these stands.

### *Relationships between the littoral and sublittoral fauna*

Thanks to the efforts of the Underwater Association, the sublittoral fauna of the Maltese islands is almost as well documented as the littoral fauna. Transects taken between  $-1$  m and  $-40$  m at Wied-iz-Zurrieq, Paradise Bay and Delimara Point provide a useful quantitative basis for comparing littoral and sublittoral distributions (Biggs & Wilkinson 1966, Wilkinson *et al.* 1967).

The data collected at Wied-iz-Zurrieq by Wilkinson *et al.* (1967) are partially summarised in Fig. 7, which shows the sublittoral distributions of species also found in the shallow sublittoral in the present study. The most frequent sublittoral species are *Columbella rustica* and *Bittium reticulatum*, the former being very common in the upper 5 m of the sublittoral, with *B. reticulatum* becoming more frequent at the base of the transect. The fact that eulittoral species are extremely rare in the sublittoral transects suggests that the base of the eulittoral represents a critical faunal division at this site. In general, there is a high degree of continuity between the shallow and deeper sections of the sublittoral, at least to a depth of 17 m, which represents the lower limit of *Columbella rustica*. The only species found consistently in the shallow sublittoral of exposed sites which is not present at depth is *Thais haemastoma*. This seems to support Pérès & Picard's (1964) contention that the upper 40 m of the sublittoral (the 'étage infralittoral') forms a unified whole, and that there is no sublittoral fringe. This is not true of sheltered sites, however.

In all the sublittoral transects, there is also an evident continuity between the densities recorded in the shallow sublittoral in the present study, and those recorded in the sublittoral transects. The only species for which density increases with depth is *Bittium reticulatum*. In



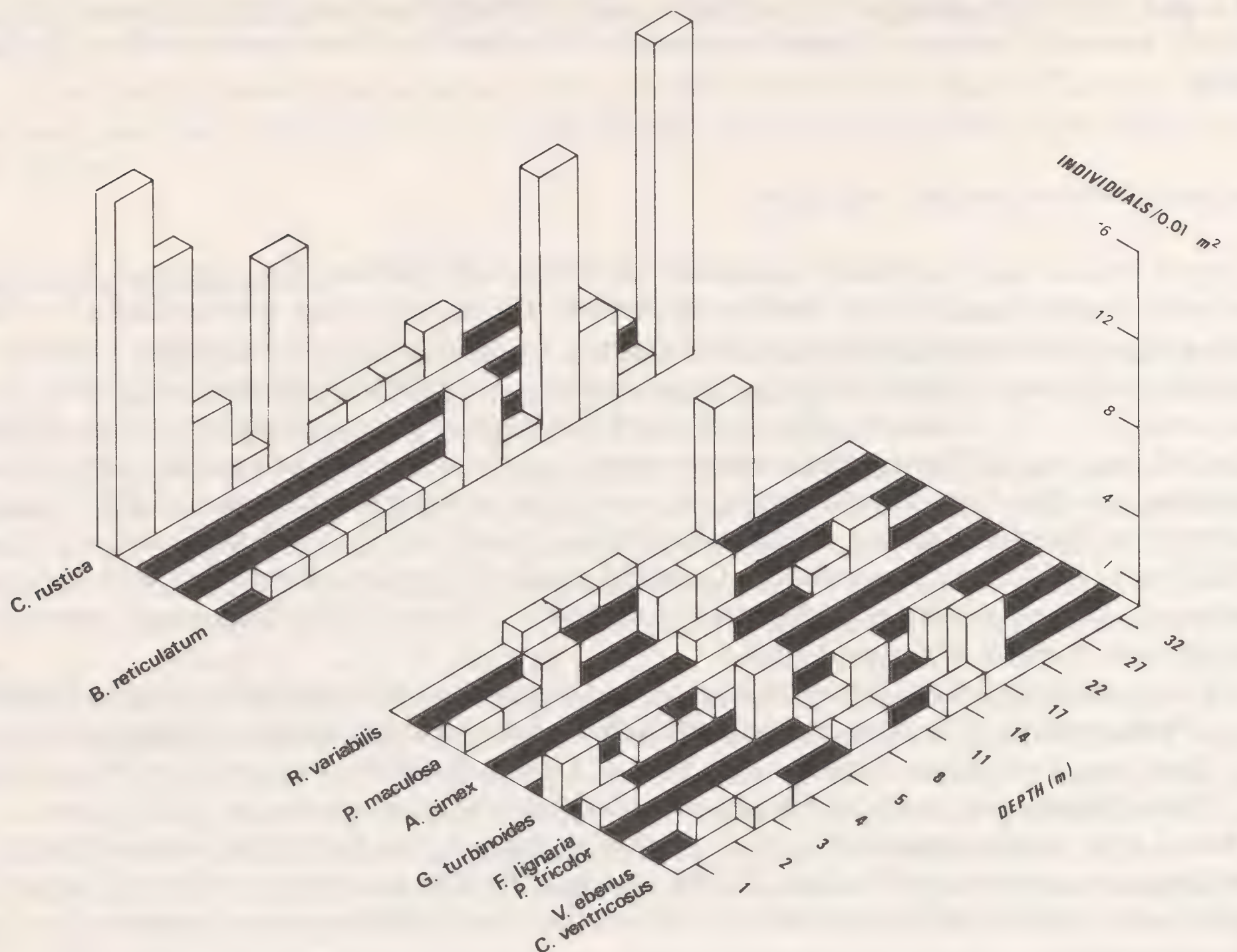


Fig. 7. Sublittoral mollusc distribution at Weid-iz-Zurrieq, after Wilkinson *et al.* (1967), transect 1. Only the most common species are represented for the sake of clarity.

terms of diversity, however, the sublittoral seems to be much richer. At Wied-iz-Zurrieq, for example, while twelve species were recorded in the littoral zone, 47 species were found in the sublittoral, and similar ratios were found for the other sublittoral transects. This would explain why so few of the species previously recorded for the islands were found live in the present study.

#### *Comparison with other Mediterranean rocky shores*

Although the Maltese rocky shore fauna and its zonal distribution is in many ways typical of the Mediterranean, some notable anomalies are present, primarily because of the uniform substrate type.

While over 400 molluscan species have been recorded in the Maltese archipelago (Cachia 1981), the comparative dearth of species recovered live in the present study shows that the common rocky shore community has a low diversity. Examination of the literature reveals that many previously recorded species have not been collected live.

The major factor inhibiting diversity seems to be the prevailing monotony of the limestone substrates, and the consequent lack of differing habitats. This uniformity is enhanced by the almost total absence of brackish water areas, owing to the lack of river runoff from the limestones. Only six brackish water species were recorded by Gatto (1912), and the



RICHARDS: MOLLUSCAN ZONATION ON ROCKY SHORES IN MALTA

TABLE 2

Species richness in the Mediterranean

Location	No. of Sites Sampled	No. of Species	Substrate	Source
Malta	1	14	Limestone	Present study
Malta	31	41	Limestone	Present study
Malta	2	26	Sublittoral Limestone	Biggs & Wilkinson (1966)
Malta	1	44	Sublittoral Limestone	Wilkinson <i>et al.</i> (1967)
Mallorca	1	13	Limestone	Richards (1982)
Marseilles	1	21	Limestone	Leung Tack Kit (1976)
N. Adriatic	1	14	Limestone	Starmühlner (1969)
Rhodes	8	23	Limestone	Fielding & Edmunds (1974)
Tunisia	1	17	Sandstone	Richards (1982)
Israel	3	44	Sandstone	Lipkin & Safriel (1971)
S. Spain	1	12	Sandstone	Reineck & Dörjes (1976)
Corsica	1	8	Sublittoral Schist	Molinier (1960)

Note: When a single site was selected from a more extensive study, the site with the most species present is cited.

oysters *Crassostrea gigas* and *Ostrea edulis* have been artificially introduced to the islands (Agius *et al.* 1977).

However, qualitative comparisons of species richness between Malta and other areas of the Mediterranean littoral show that while the Maltese species pool is low, species richness at individual sites may be comparatively high. Table 2 shows, for example, that the Maltese species pool (41 species from 31 sites) is impoverished relative to sandstone shores in Israel (44 species from 3 sites, Lipkin & Safriel 1971) and Tinos in the Aegean (23 species from 3 sites, Fielding & Edmunds 1974). In contrast, individual sites in Malta exhibit similar levels of species richness to those found in other limestone areas, such as northern Yugoslavia and the Marseilles region, and the figures for all these areas are higher than for sandstone or volcanic substrate sites. Thus the patterns of diversity found in Malta seems to be controlled to a large extent by substrate type. Whilst limestone provides varied micro-habitats and exhibits high species richness at individual sites, the lack of different lithologies in Malta restricts the size of the overall species pool.

In spite of these differences in species richness, the zonation pattern found in Malta is similar to those in other areas of the Mediterranean, particularly in the eastern basin. Detailed work on the trochids of the Marseilles area by Huvé (1956) and Regis (1969) revealed similar zonal distributions as those found in Malta. *Monodonta turbinata* was found between +0.25 m and -0.05 m on exposed shores, with maximum densities of 200/m<sup>2</sup>, while *M. articulata* occurred between +0.20 m and -0.20 m, with maximum densities of 250/m<sup>2</sup>. In sheltered pools, *Gibbula divaricata* and *G. richardi* were present, a similar association to that found on boulder shores in Malta. The only major differences in distribution between Marseilles and Malta seems to be the restriction of *Monodonta articulata* to sheltered shores in Malta.

A study of the limestone coast of northern Yugoslavia by Simunović (1970) also shows similarities to the Maltese zonation. *Littorina neritoides* is present up to +4.5 m on exposed shores, attaining maximum densities of 480/m<sup>2</sup> at +1.5 m. This is, however, an order of magnitude lower than the maximum densities recorded in Malta. *Chthamalus stellatus* and



*Patella lusitanica* dominate the upper eulittoral zone, with the latter reaching densities of 200/m<sup>2</sup>, also lower than in Malta. *Monodonta turbinata* is found just above MSL at 200/m<sup>2</sup>, but vermetids are absent. In the sublittoral fringe, *Pisania maculosa* and *Conus ventricosus* were found at about 16/m<sup>2</sup>, while *Cerithium rupestre* and *Gibbula divaricata* are dominant on sheltered shores.

Data given by Huvé (1957) for dolomitic shores at Cape Matapan in Greece show the same zonation pattern as well as similar densities for most species. At about +1 m, *Chthamalus stellatus* and *Littorina neritoides* may attain densities of 5,000/m<sup>2</sup>, while at +0.50 m *Patella lusitanica* reaches 500/m<sup>2</sup>. Thus, where the biomass of Maltese shores may be lower than on Mediterranean shores with different lithologies, it is within the range expected for limestone shores, while also exhibiting a high level of species richness.

Comparison of Maltese zonation pattern with those from other areas is difficult owing to the predominant use of the Pérès & Picard (1958) zonation scheme. This does not recognise a sublittoral fringe or divide the littoral zone so finely as the Lewis (1964) scheme.

The only previous study made using the Lewis (1964) scheme was that conducted on the Israeli coast at Mikhmoret by Lipkin & Safriel (1971). Working mainly on moderately or extremely exposed sandstone shores, they found no molluscan evidence for a sublittoral fringe. In Malta, a sublittoral fringe can be identified, but only at sheltered sites. Studies in Corsica (Moliner 1960) and Yugoslavia (Simunović 1970) also indicate the existence of shallow sublittoral associations of *Cerithium rupestre* and *Gibbula divaricata* in sheltered locations. This seems to suggest that a discrete sublittoral fringe may be found in the Mediterranean only at sheltered sites. One possible explanation is that the small tidal range allows repeated emersion of the upper sublittoral at exposed sites with large wave amplitudes, so that the transition from eulittoral to sublittoral conditions is sharper than at sheltered sites.

It is also interesting to note that *Vermetus triqueter* was found to occur at about -0.50 m for all exposure conditions at Mikhmoret. In Malta this species occurs mainly on exposed shores, and tends to increase slightly in vertical range with increasing exposure, with the bulk of the population always found at about MTL. This may point to more severe desiccation at Mikhmoret, but does not explain the lack of overall range extension with increasing exposure. Such differences are important in view of the frequent use of the vermetids as sea-level indicators in the Mediterranean.

In spite of the apparent absence of a sublittoral fringe at Mikhmoret, Lipkin & Safriel (1971) concluded that the Stephenson & Stephenson (1949) scheme was applicable to the Mediterranean coast of Israel, and the present study has further shown that the modified scheme proposed by Lewis (1964) is applicable to the limestone shores of Malta and probably to many other areas of the Mediterranean.

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## TAXONOMIC SPECIES LIST\*

**Polyplacophora**

*Chiton olivaceus* Spengler 1797

**Gastropoda**

\**Fissurella nubecula* (L. 1758)

\**Patella aspera* Lamarck 1819

*P. caerulea* L. 1758

*P. lusitanica* Gmelin 1791

*Monodonta articulata* Lamarck 1822

*M. turbinata* (Born 1780)

\**Jujubinus exasperatus* (Pennant 1977)

\**Gibbula ardens* (Von Salis 1793)

\**G. nivosa* (Adams 1851)

*G. turbinoides* (Deshayes 1832)

*G. richardi* (Payr., 1826)

*G. divaricata* (L. 1758)

*G. varia* (L. 1758)

*Clanculus cruciatus* (L. 1758)

\**C. jussieui* (Payr. 1826)

*Littorina neritoides* (L. 1758)

\**L. punctata* (Gmelin 1791)

\**Hydrobia ulvae* (Pennant 1777)

*Alvania cimex* (L. 1758)

\**A. scabra* (Philippi 1844)

*Rissoa variabilis* (von Mühlfeldt 1824)

*Vermetus triqueter* (Bivona 1832)

*Serpulorbis arenaria* (L. 1758)

*Bittium reticulatum* (Da Costa 1778)

*Cerithium vulgatum* (Brug. 1792)

*C. rupestre* Risso 1826

\**Epitonium commutatum* (Monterosato 1877)

*Trunculariopsis trunculus* (L. 1758)

*Ocenebrina edwardsi* (Payr. 1826)

*Thais haemastoma* (L. 1767)

\**Corallophila meyendorffi* (Calcara 1845)

\**Mitrella gervillei* (Payr. 1826)

*M. scripta* (L. 1758)

*Columbella rustica* (L. 1758)

\**Buccinulum corneum* (L. 1758)

*Pisania maculosa* (Lamarck 1822)

*Hinia costulata* (Reneiri 1804)

\**H. incrassata* (Ström 1768)

*Fasciolaria lignaria* (L. 1758)

*Pusia tricolor* (Gmelin 1791)

*Mitra fusca* (Swainson 1829)

*M. ebenus* (Lamarck 1811)

*Conus ventricosus* (Gmelin 1791)

**Bivalvia**

\**Arca noae* L., 1758

*Barbatia barbata* (L. 1758)

*Mytilus galloprovincialis* Lamarck 1819

*Lithophaga lithophaga* (L. 1758)

\**Ostrea stentina* (Payr. 1826)

\**Cardita calyculata* (L. 1758)

\**Glans trapezia* (L. 1767)

**Crustacea**

*Chthamalus stellatus* (Poli 1795)

*Balanus* spp.

\*not mentioned in the text



# REDISTRIBUTION AND LOCAL RECOLONISATION BY THE FRESHWATER PEARL MUSSEL *MARGARITIFERA MARGARITIFERA* (L.)

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(Accepted for publication 19 March 1983)

*Abstract:* *M. margaritifera* is shown here to be a largely sedentary animal, which can move short distances, however, if its habitat changes. It requires a stable substrate of coarse sand, where it burrows to varying depths, and it does not occur in streams where the substrate is substantially resorted by torrents. In these it fails to establish and is washed away. Recolonisation of denuded areas can only be achieved very slowly by adult mussels and the main source of colonists is certainly young mussels being released from host fish. When large mussels suddenly reappear in denuded areas it is probable that these are specimens which were previously completely buried and have since burrowed up into view.

## INTRODUCTION

The freshwater pearl mussel, although usually regarded as a sedentary animal, has the ability to burrow and to move about slowly and rather inefficiently (Davis and Fuller 1981). The mechanism by which this is achieved is described by Trueman (1968). However there is no agreement about whether the mussels do ever move significant distances naturally (although Boycott and Bowers (1898) assert that they do) and this is generally discussed with reference to two main problems. First of all whether young mussels occupy a different substrate type to older mussels, moving between these substrates as they grow; and secondly whether mussels can redistribute themselves and recolonise areas which have become vacant, either through natural displacement or through man's pearl fishing activities, (Jackson 1925, McCormick *pers. comm.*). This study aims to provide evidence to answer these questions.

A population of the freshwater pearl mussel was studied in the Stac Burn, Iverpolly N.N.R., Wester Ross from 1978 to 1981. Here two areas were artificially denuded of mussels and recolonisation was monitored; the mussels in two other areas were mapped precisely each month so as to observe natural movements; and marked mussels were moved to a tributary stream which was torrential and naturally devoid of mussels, so as to observe whether mussels moved more there than in the Stac Burn. It was hoped to distinguish between voluntary and involuntary movements of mussels by close comparison between their movements and those of similarly sized stones.

## STUDY AREA AND METHODS

The Stac Burn, Iverpolly N.N.R., Wester Ross (NC 0812) is a typical Scottish west-coast mussel habitat. It has an abundant mussel population, which has apparently been fished only occasionally, and is small enough to be accessible even in winter high-water

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TABLE 1

Movement of mussels into two areas artificially denuded of them in the Stac Burn, Inverpolly N.N.R., Wester Ross.

	Date of observations <sup>1</sup>																					
	Sept 1978	10	12	$\frac{2}{79}$	3	4	5	6	7	8	9	10	11	$\frac{1}{80}$	2	3	5	6	8	9	11	$\frac{3}{81}$
Area 1																						
Total No. found in area	0	0	2	1	1	4	5	5	6	8	7	8	7	7	7	8	8	9	9	10	12	10 <sup>2</sup>
No. found in 0.50 m edge of area	0	0	1	1	1	2	2	2	2	3	3	3	3	3	3	3	3	4	4	5	6	5
Area 2																						
Total No. found in area	0	6	4	5	4	7	8	8	10	9	10	11	11	11	9	10	10	11	11	10	10	12 <sup>2</sup>
No. found in 0.50 m edge of area	0	4	2	3	3	4	4	4	5	5	5	6	6	6	4 <sup>3</sup>	5	5	6	6	6	6	8

1) Note: time intervals are not equal.  
2) Includes central group of up to 6 small, buried mussels, difficult to locate and immobile.  
3) 2 marginal mussels moved out of area.

Area 1—1.5 m × 2 m, Area 2—2 m × 3 m. Both denuded of mussels in September 1978

levels. It is approximately 3 m wide, generally 0.20–0.50 m deep and flows from a small loch to join the River Polly. Its substrate is a variable mixture of coarse sand, gravel, stones and some boulders, and mussels are found throughout it except in one or two very small sandy areas. Its substrate composition, and that of its main tributary, was assessed subjectively according to a modified Wentworth classification (Wentworth 1922).

1. *Recolonisation experiments*

Two areas, which were easily delimited by reference to emergent marker stones, and which contained mussels at a representative density for the Stac Burn, were denuded of all mussels as far as possible. In the immediately surrounding areas normal mussel populations remained and there was no barrier of any sort between these populations and the denuded areas.

The denuded areas were observed at intervals for 30 months from September 1978 and all mussels within them mapped to the nearest 30 mm. One of these areas was approximately 1.5 m × 2 m (area 1 of Table 1) and the other 2 m × 3 m (area 2 of Table 1).

2. *Observations of natural mussel movements*

In October 1978 two areas were chosen, one 1.5 m × 2.5 m (area 1 of Table 2) and one 2 m × 2.5 m (area 2 of Table 2), each of which contained a representative density of mussels (about 65–70 each). These mussels were moved so that the mussels were approximately evenly distributed throughout the areas and were then left to re-establish themselves. The mussels in one area were mapped from October 1978 to March 1981 and in the other from August 1979 to November 1980. In each case mussels were located at least to the nearest 30 mm and could usually be located more precisely by reference to the position of stones.

3. *Mussel loss from a torrential stream*

In September 1979, 20 mussels were marked using a technique described by Young and Williams (1983) which does not harm the mussels. These were then placed in apparently suitable areas 30 m up a tributary of the Stac Burn. The tributary is similar to the Stac Burn



# YOUNG AND WILLIAMS: FRESHWATER PEARL MUSSEL

TABLE 2.

Movement of mussels within two mapped areas of the Stac Burn, Inverpolly, N.N.R., Wester Ross.

	Date of observations <sup>1</sup>																						No's and % unmoved
	Oct 78	12	<u>2</u> 79	3	4	5	6	7	8	9	10	11	<u>1</u> 80	2	3	5	6	8	9	11	<u>3</u> 81		
<i>Area 1</i>																							
No's in area	65	58	56	58	62	66	70	74	75	74	76	75	74	72	74	76	75	73	68	69	68	11/79 to 11/80	
No's moved in interval	—	10	8	12	4	5	7	10	6	4	4	3	2	2	2	5	8	14	13	9	2	18	
% moved in interval	—	17	14	21	6	8	10	14	8	5	5	4	3	3	3	7	11	19	19	13	3	= 26%	
Max <sup>m</sup> distance moved—cms	—	20	20	15	15	10	15	25	20	10	20	5	5	5	5	10	20	25	20	15	5		
<i>Area 2</i>																							
No's in area											71	71	70	68	66	66	67	70	69	66	65	64	11/79 to 11/80
No's moved in preceding interval											3	2	2	6	1	0	2	1	1	8	8	0	20
% moved											4	3	3	9	2	0	3	1	1	12	12	0	= 31%
Max <sup>m</sup> distance moved—cms											10	15	10	20	10	—	15	15	25 <sup>2</sup>	20	20	—	
Low water											L	L	L	L		L		L	L	L	L		

1) Note: time intervals not equal

2) track clearly visible

Area 1—1.5 m × 2.5 m, Area 2—2 m × 2.5 m. Mussels in both areas distributed and mapped in October 1978

Maximum distance moved=25 cms

Maximum proportion moving=21% (Area 1, March 1979) or 19% (Area 1, August & September 1980)

Average proportion moving=8%

in most respects, except that there is no loch in its catchment area and so it is subject to swift rises in water level, leading to more torrential conditions. At intervals for 14 months these marked mussels were searched for and mapped. No mussels occur naturally in this tributary. A further batch of 20 was similarly introduced and subsequently observed in March 1980.

## RESULTS

### *Recolonisation experiments*

The results of the recolonisation experiments, that is the number of mussels found in each of the two denuded areas, is shown in Table 1. It should be noted that in each case some mussels appeared suddenly more than 0.50 m from the edge of the areas. This is a greater distance than any mussels were shown to move in similar time intervals in the 2nd experiments (see below) and these mussels were often seen to be almost wholly buried. It is thought therefore that they survived the denudation and only became apparent when they burrowed less deeply.

Consequently a more realistic figure for the number of invading mussels is shown by the number found within 0.50 m of the area's edge. In some cases the maps show in detail the slow progress of these mussels into the edge of the area, but in no case did such a mussel progress beyond this edge zone. One was found first unburied on the substrate and only subsequently became buried at that site, it seems likely it was washed in from upstream.



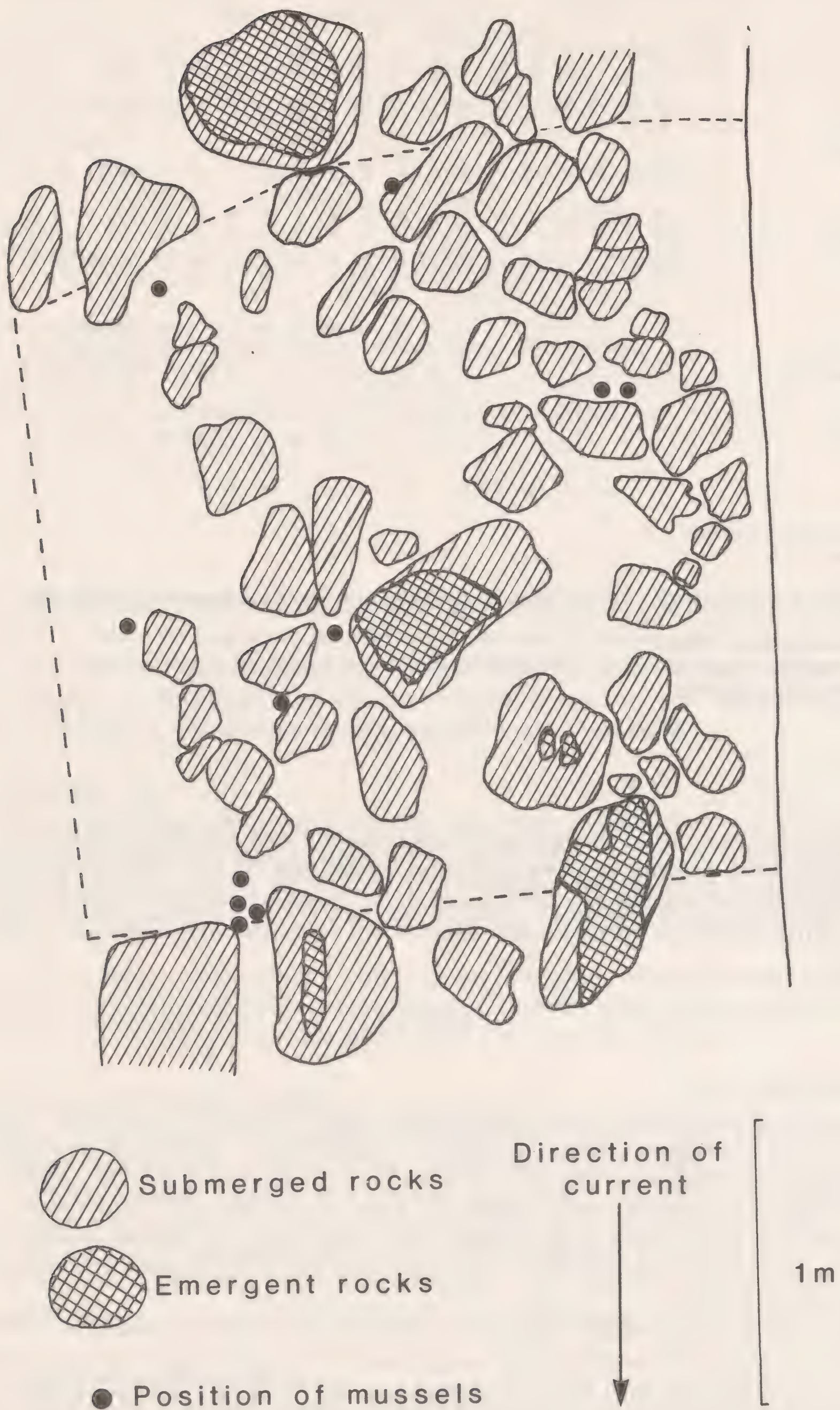


Fig. 1. Recolonisation area 2. The position of mussels in March 1981.



From Table 1 it can be seen that 5 and 8 mussels respectively invaded the edge of the denuded areas in 30 months. (The original number of mussels found in the whole of these areas was about 50 and 70 mussels respectively). Such invasion would only be possible where sand patches are continuous between adjacent areas except for rare occasions when mussels are washed in.

Although the number of invading mussels was too low to allow statistical analysis there was no indication that the invasion was occurring predominantly from any particular direction. Fig. 1 shows the position of the mussels in Area 2 at the completion of the observations in March 1981.

The results show that not all mussels were found each month and this occurred because of the variable depth at which mussels buried and the variable viewing conditions. High, turbid water and overcast conditions sometimes made searching difficult.

#### *Observations of natural mussel movement*

Table 2 shows the number of mussels found in each mapped area and the number definitely observed to have moved between each time interval. It also lists the maximum distance moved and the number remaining completely stationary between November 1979 and November 1980.

The fluctuation in total numbers found within the areas illustrates the difficulty of finding mussels, which often bury deeply, under varying stream conditions. It certainly does not represent movement of mussels in and out of the areas.

In both areas the mussels were moved to an approximately even distribution at the start of the experiment. Consequently the initial movements may have been resettling; however, this phase (if it existed) was obviously completed by April/May 1979 when the proportions moving were very low. Although Area 2 was established in October 1978 it was not mapped adequately until August 1979 and so the observations made up till then have been discarded. To avoid both these complications the estimates of numbers remaining immobile were made from November 1979 to November 1980.

The proportion of mussels moving each month varies from 0 to 21% of those present and up to 31% remained unmoved over a period of one year. In most cases movement is of 50 mm or less but some mussels moved up to 0.25 m in one month. (Laboratory observations have shown that mussels can move 25 cms in less than 1 day under some conditions).

It is clear that the mussels can redistribute themselves over the areas quite actively, presumably in response to changing conditions. These experiments and other casual observations between May 1978 and May 1981 suggest, however, that some mussels rarely, if ever, move. The detailed maps show that these static specimens seem to be those between or behind rocks.

Observed occurrences of very low water are shown in Table 2 but there seems to be no real relationship between them and times of maximum movement. The suggestions from the table that a peak of movement occurred simultaneously in both areas in August and September 1980 supports the view that movement is governed by some overall environmental variable, but this factor remains unidentified.

Observations showed almost no change in the position of even the small stones over the period of observation. Many spates occurred between October 1978 and March 1981 but the substrate was generally unaffected by them.

Fig. 2 shows the position of mussels in Area 1 at the completion of the observations in March 1981.

#### *Mussel loss from a torrential stream*

Table 3 shows observations on the loss of marked mussels from a torrential tributary of the Stac Burn. It is clear that a high proportion of the mussels move or are moved out of the



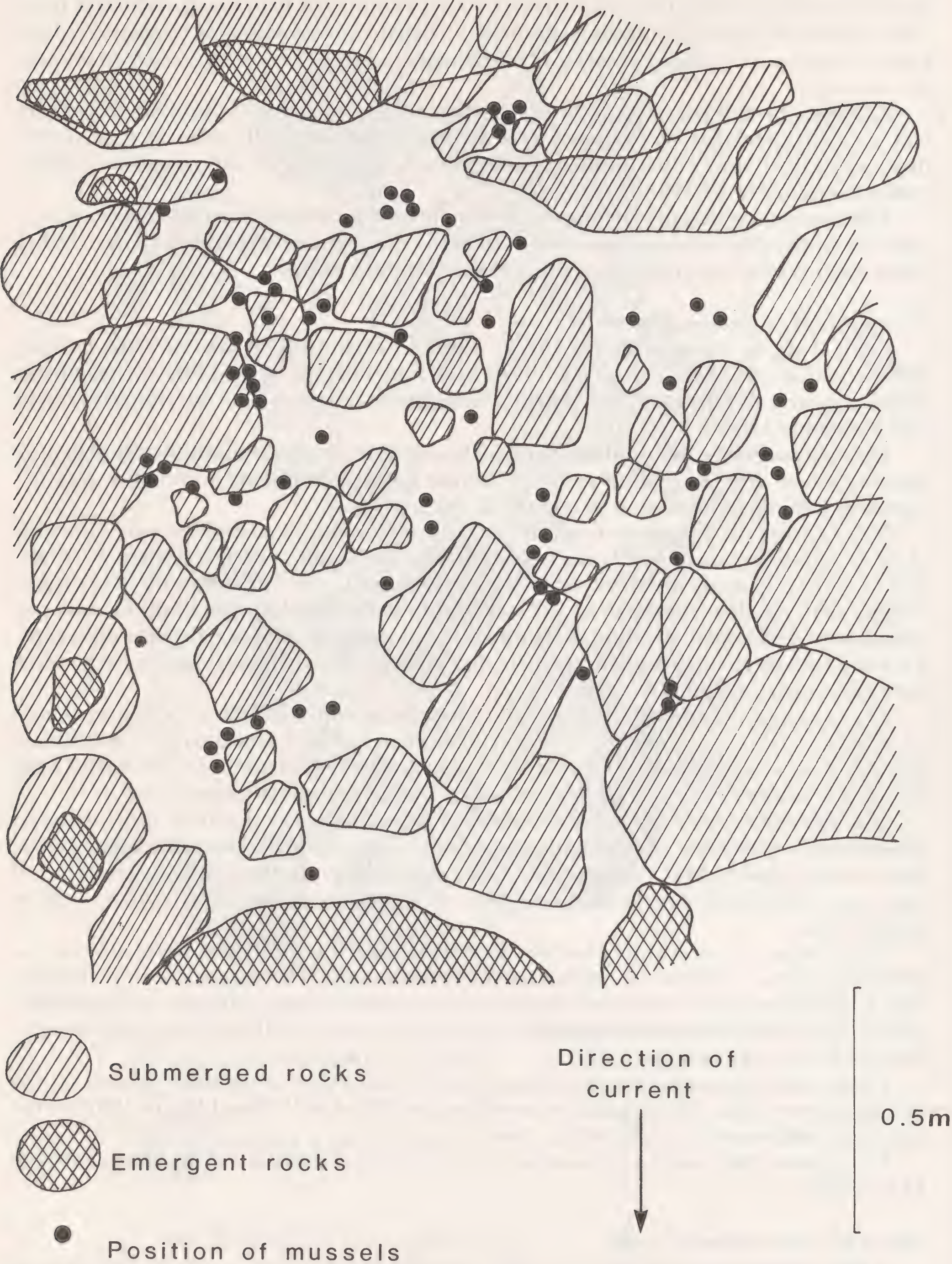


Fig. 2. Mussel movements observation area 1. The position of mussels in March 1981.



YOUNG AND WILLIAMS: FRESHWATER PEARL MUSSEL  
TABLE 3

The loss of marked mussels from a tributary of the Stac Burn, Inverpolly, Wester Ross.

Dates of observations								No. & % lost <sup>1</sup>
	Sept 1979	Oct 1979	Feb 1980	Mar 1980	May 1980	June 1980	Nov 1980	
Batch 1								
No's of mussels present	21	13	11	14	14	11	5 <sup>1</sup>	15,=71%
Notes		3 of these found dis- placed and returned		3 found down- stream		1 extra found dead downstream		
Batch 2								
No's of mussels present				20	19	18	9 <sup>1</sup>	10,=50%

<sup>1</sup>Two found with missing tags so unattributable to Batch, 1 of these has therefore been attributed to each batch

Losses: Batch 1 71% in 14 months, Batch 2 50% in 8 months

c.f. Maximum possible losses reported in Areas 1 and 2 in Table 2; area 1 11% (8 mussels) in 29 months, area 2 10% (7 mussels) in 15 months.

area of introduction very quickly and some of these were subsequently recovered 10–20 metres downstream. There was a 71% loss from one batch in 14 months and a 50% loss from the other in 8 months. This displacement contrasts so markedly with that noted in Table 2 for the Stac Burn that it seems likely to be a genuine loss due to mussels being washed away. Areas of coarse sand, such as are frequent in the mussel-inhabited Stac Burn, are much less frequent in the tributary, but there are no significant differences in the water chemistry (Purser *pers. comm*) and Brown Trout are available as glochidial hosts in both. Unfortunately no direct observations were made on the stability of the substrate in the tributary, however subjective assessments were made of the proportion of different substrate types on a modified Wentworth scale. Table 4 lists these proportions and shows the more torrential nature of the tributary by the greater proportion of coarse sediments.

DISCUSSION

It is clear that mussels can move, in suitable substrate, and can recolonise depopulated areas or redistribute themselves after disturbance. It is equally clear that such movement and redistribution is very slow and could not contribute significantly to the recolonisation of a large stream area after its denudiation. (Boycott and Bower's (1898) observations that a mussel can move 12–15 feet/day has not been supported by evidence from any later studies). Recolonisation must therefore be achieved by the establishment of young mussels brought to the area as glochidia on their host fish. Only in the torrential tributary were mussels carried passively by the current for any distance, except for 1 specimen noted from Area 2 in the removal experiments. Adult mussels moving slowly to new areas could obviously not pass rock barriers (except very rarely when being carried passively by the current; it seems inconceivable that they can climb like *Sphaerium* sp.) and in cases where rapid partial replacement of large mussels has



TABLE 4

Subjective assessments of the substrate types of the Stac Burn, Inverpolly, Wester Ross and its main tributary.

Substrate types (modified Wentworth scale)	Stac Burn % composition	Tributary % composition
Silt		
Sand	30	<1
Gravel	10	<5
Stones	30	60
Boulders	30	30
Bedrock	<1	5

been observed after areas have been fished out (McCormick *pers. comm.*, Cranbrook 1976) it is our view that mussels previously buried, and so not removed, have pushed up into view.

When mussels first leave their fish hosts they are only 0.5 mm in diameter and probably establish themselves immediately in coarse sand. At this stage they (and the sand) may be redistributed passively by water currents and this method may contribute to the recolonisation of denuded areas. It has been suggested that mussels move most at very low water (Bauer *pers. comm.*), moving to deeper water to avoid becoming stranded, or to avoid warm deoxygenated water, however our evidence does not really support this contention. If there is a time of maximum movement it seems to be autumn which is certainly not a time of low, warm water in western Scotland. Instead we have often observed spates at that time of year.

Furthermore we have observed mussels being stranded and sometimes these have moved but sometimes not. Our evidence is insufficient to link movement with any special environmental factor.

We suggest that mussels are sedentary, by preference, if they find a suitable area of coarse sand in which to burrow and which remains stable. They do seem to burrow more deeply or more shallowly occasionally but the reasons for this are not clear and natural changes in the depth of the sand may contribute to the observation. However if the mussel's position becomes unsuitable, either due to low water, a change in the substrate or whatever else, then they have the capacity to move, at least short distances, to a new position. This movement is only possible across areas of suitable substrate except for the occasional involuntary washing out of mussels, and so recolonisation must depend mainly on invasion of young mussels from fish. Eager (1977) suggests that it is mainly mussels inhabiting the slower rivers which move and that their generally rounded and less 'beaked' shape (in relation to mussels from faster rivers) is more suitable for movement.

One factor influencing whether mussels persist in a stream is obviously the stability of the substrate in relation to the current speed and some otherwise suitable streams are clearly too torrential. Altnoder (1926) measured the gradient of various streams in Germany and found a good correlation between the gradient and the presence of mussels. In streams where the gradient averaged 2.36% mussels were absent, whereas in streams where they were present the average gradient was 1.36%. He does not suggest whether the effect of the increased gradient acts directly on the mussel or indirectly through instability of the substrate. This study suggests that a direct effect on the mussels may occur but, of course, the substrate may also be affected as well and this would have an indirect effect on the mussels which we have not attempted to measure.



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## REVIEW

SEASHELLS OF OMAN by Donald and Eloise Bosch, edited by Kathleen Smythe, 206 p. of which 162 are of photographs in colour, Longman Group Ltd 1982, price £17.

This very handsomely produced book is a welcome addition to books on shells of specific areas. Its contents, after publication details, are a list of contents, a preface, a foreword by R. Tucker-Abbott, three pages on taxonomy, a map of the Sultanate of Oman, a page on 'Geological History Shaping Molluscan Life', a page on Plankton, two on 'Thumbnail Answers to Common Questions', two on Cleaning Shells in Oman and one on 'How Big? Where Found? What Arrangement?'. Pages 26 to 197 deal with the molluscs of Oman in their classes, subclasses, orders, families and sub-families. Gastropods take up 114 pages, Scaphopods and Chitons one each, Bivalves 46 and Cephalopods two.

The names of shells are given with authors' names, in brackets where appropriate, and dates, for which congratulations are due. Too many books omit dates. The descriptions of the shells are very short but concise and the photographs are in nearly all cases very good indeed and helpful for identification. Occasionally the colour is not right, due perhaps to the printing. The descriptions include size, habitat and whether commonly found or rare in Oman. It would have been helpful, though requiring a great deal of research, if the known ranges beyond Oman had been included.

The photographs are printed to show the shells as effectively as possible for identification, but as a result shells on the same or facing pages are often quite out of proportion: as examples *Cypraea nebrites*, *C. moneta* and *C. mauritiana* are illustrated on the same page and the picture of *C. mauritiana* is only marginally bigger than those of the other two, while *Argonauta argo* and *A. hians* on facing pages are the same size. Certainly the average sizes are given in the descriptions and one would lose detail if they were illustrated in proportion, but the effect is nevertheless a little odd.

The authors say that they make no claim to present all the living molluscs of Oman, but infer that all they have collected in their twenty-five years in the Sultanate are included. It may be presumptuous to say so, but I cannot escape the feeling that the molluscan fauna of such a large area in the Indian Ocean must be somewhat greater than the 368 species included in the book. For example, are there no *Littorina* species in Oman? Only one scaphopod is illustrated and described, and it is not stated whether or not other species are found, while although only one chiton is included, it is acknowledged that several others have been found although most are small and present identification problems—a fair comment. (The Editor has told me that many more species have been found by the authors since they wrote the book some two years ago.)

The shell book without errors has yet to be published, but this book does not seem to have more than its fair share. However the *Epitonium* on page 51, given as 'Up to 65 mm' must surely be *E. scalare* and not *E. pallasi*; *Hindsia bitubercularis* on page 100 is a junior synonym of *Nassaria acuminata* (Reeve, 1844); on the same page the bottom picture is not of *Cantharus spiralis* but of *C. erythrostomus* Reeve 1846, on page 113 *Mitra pretiosa* (Reeve 1844) is not correct and should be *M. papilio* (Link, 1807); *Cancilla isabella* (Swainson 1840) page 115 is only found in the area of Japan and Taiwan, but I would hesitate to give this shell its correct name; the four shells illustrated as *Cypraea grayana* (Schilder, 1930)—the upper left and lower right specimens look to me more like *Cy. histrio* (Gmelin, 1791) and I would have expected both species to be found off Oman.

On page 47 there is an illustration of *Telescopium telescopium* (Linneus 1758). Apart from the photograph being an example of poor colouration (the shell should be a very dark grey—almost black), this species where found—in such places as mangrove swamps—is always found in abundance. The authors say 'We have found it only near Muscat, dead. Very rare'. I can only believe therefore that it must have been washed up from outside Oman and should not be classed as an Omani species.

I do not pretend that this list of corrections is exhaustive, especially as I am quite unqualified to comment on Bivalves.

Since the book was written the *Ancilla* species on page 111 has been named *Aboschi* (Kilburn, 1980).

For the price of around £17, I would recommend this book to anyone who may be interested in the shells from the North-West Indian Ocean, or who likes to own well-produced shell books.

PETER OLIVER



# DISTRIBUTION OF LAND AND FRESHWATER MOLLUSCA IN CORSICA

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(Accepted for publication 16 October 1982)

**Abstract:** A list of the land and freshwater Mollusca of Corsica is presented, based on the literature and collections made during 1977. The distribution of each species is listed for the 50 km squares of the U.T.M. grid. The following species are reported from Corsica apparently for the first time: *Ferrissia wautieri* (Mirolli), *Columella aspera* Waldén, *Toltecia pusilla* (Lowe), *Punctum pygmaeum* (Draparnaud), *Vitrea contracta* (Westerlund), *Milax nigricans* (Philippi), *Limax valentianus* Férussac, *Deroceras laeve* (Müller), *Deroceras panormitanum* (Lessona & Pollonera), *Euconulus alderi* (Gray) and *Pisidium personatum* Malm.

## INTRODUCTION

An extensive literature exists on the land and freshwater Mollusca of Corsica but much of it is old and difficult to locate (cf. Caziot and Fagot 1909). Radically different approaches to systematics by different authors have created difficulties of identification even when the appropriate literature can be assembled. It is thus not surprising to find frequent mistakes due to misinterpretation of complex synonymies and mistranslation in the existing literature.

Brief visits to Corsica in April and December 1977 allowed a modest collection of Mollusca to be made. Identification of this material showed that species of small size had often been overlooked by earlier workers and slugs had been neglected. My original intention was to publish only an annotated list of these additions to the Corsican fauna. However, the commencement of the European Invertebrate Survey—a plan to map the distribution of invertebrates throughout Europe on the basis of the 50 km squares of the U.T.M. grid (cf. Kerney 1976)—has encouraged me to prepare a critical summary of Corsican distributional records from the literature as well as my own observations.

The list that has resulted can be no better than our understanding of taxonomy, especially species-limits, in each of the groups studied. It is evident that systematic knowledge of some groups is quite inadequate and the Hydrobiidae, most slug genera, some genera of Zonitidae and the Helicellinae pose particularly difficult problems. Little progress has been made in understanding some of these difficult groups since Germain's masterly 'Faune de France' volumes of 1930 and 1931, despite the development of the biological species concept since that time (Mayr 1942, Cain 1954). Most of the hundreds of unnecessary specific and generic names created on the basis of trivial differences of shell form by followers of the 'Nouvelle Ecole' of the late nineteenth and early twentieth centuries were placed in synonymy by Germain but some have perhaps been wrongly allowed to survive to the present day. This summary attempts to bring Germain's listing up to date from taxonomic and nomenclatural points of view, to correct various omissions and mistakes, and to add some new information.

For each species the modern name, its author and year of publication are listed, followed by a list of distributional records for the 50 km squares of the U.T.M. grid. Within each 100 km square the four 50 km squares have been designated by the numbers 1, 2, 3 and 4 (see Fig. 1) following the system used for the *Atlas Florae Europaeae*; this system avoids potential confusion of references to 50 km and 10 km squares. The list of grid squares is followed by a

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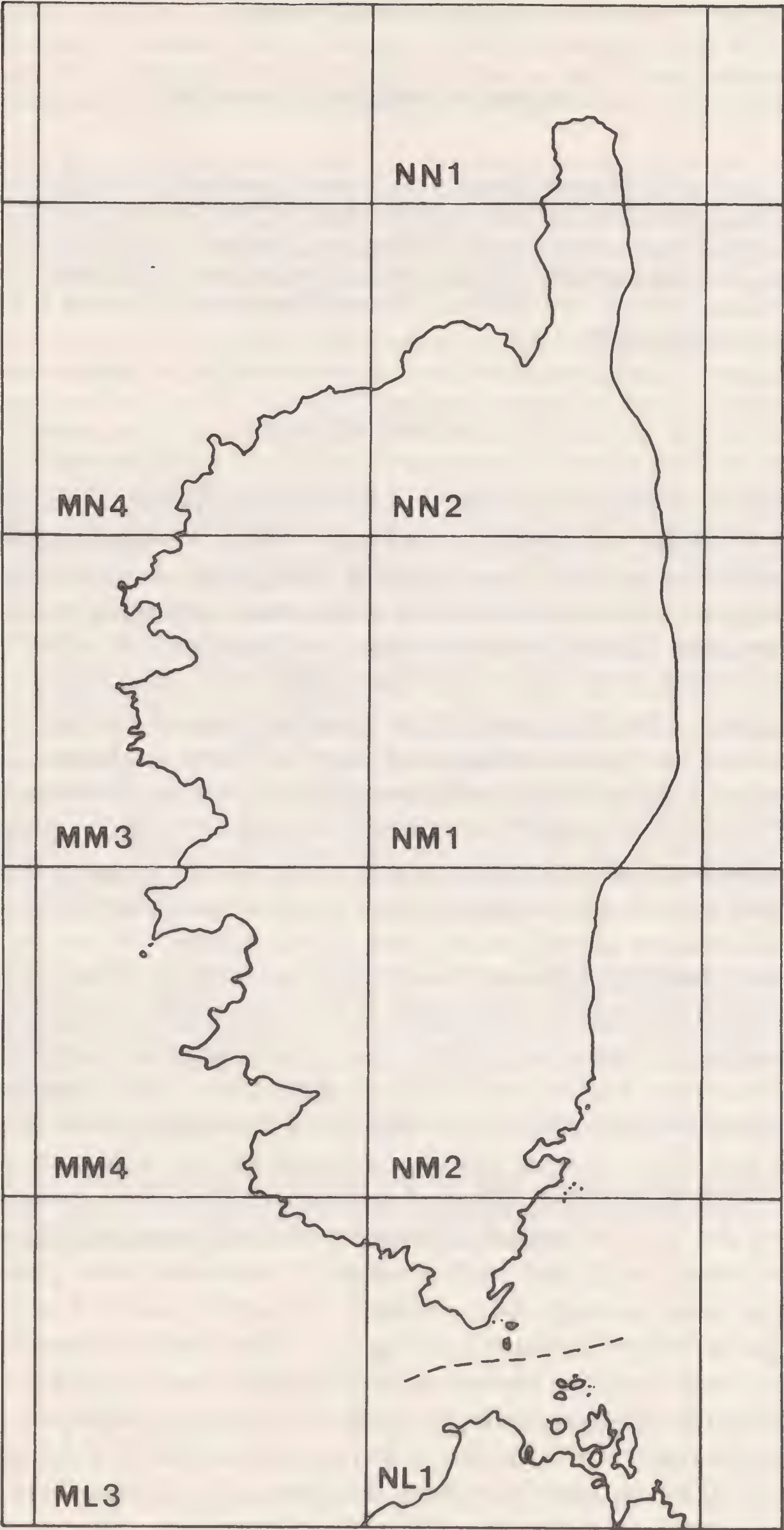


Figure 1. Map of Corsica to show 50 km squares of the U.T.M. grid.



list of sources (and citations) of the records that are considered acceptable ('DTH' indicates my own records) and often by comments on systematics or problems of identification. Species that appear to be hitherto unrecorded on Corsica are marked with an asterisk; species thought to be endemic to Corsica are marked with a dagger†; species for which no reliable Corsican record is known or which are of dubious taxonomic validity are listed in square brackets.

There can be little doubt that further fieldwork will add to the list and produce many new distributional records while systematic research will modify treatment of some groups. An Appendix gives a list of the principal collections and publications with the present location of the specimens when it is known. Some collections and publications have probably been overlooked and I would be grateful to know of these.

## SYSTEMATIC LIST

### Prosobranchia

#### Neritidae

[*Theodoxus fluviatilis* (Linnaeus 1758): Caziot (1902) and Germain (1931) quote Requien (1848) as having recorded this species for Ajaccio, but Requien makes no mention of it.]

*Smaragdia viridis* (Linnaeus 1758): MM4 (Requien 1848; DTH.).

#### Cyclophoridae

†*Cochlostoma cyrniacum* (Mabille 1869): NN2 (Mabille 1869, Caziot 1902, Germain 1931); Germain (1931) comments that this may be a form of *C. patulum* (Draparnaud 1801); Requien (1848, p. 49) also reported '*Cyclostoma obscurum* Drap.' [from NN2] but this identification may be questioned (cf. Caziot 1902, Germain 1931, p. 584).

#### Valvatidae

*Valvata cristata* Müller 1774: NL1, NM1 (Caziot 1902, Germain 1931); an earlier record (Shuttleworth 1843) gives no locality and it is doubted by Caziot (1902).

[*Valvata piscinalis* (Müller 1774): listed from Ajaccio [MM4] by Requien (1848) and for Corsica without details by Alzona (1971); confirmation of these records is desirable (cf. Caziot 1902).]

#### Pomatiidae

*Pomatias elegans* (Müller 1774): MM4, MN4, NL1, NM1, NN2 (Payraudeau 1826, Requien 1848, Caziot 1902, Büttner 1926, Germain 1931); Caziot (1902) and Germain (1931) discount old records of *P. sulcatus* (Draparnaud 1805).

#### Hydrobiidae

*Hydrobia acuta* (Draparnaud 1805): NN2 (Requien 1848, Caziot 1902, 1908, Germain 1931; DTH.); I follow Germain (1931) in treating *H. procerula* (Paladilhe 1869) as likely to be a form of this species (cf. Alzona 1971). The single shell found near Bastia [NN2] by Caziot (1902) and identified as *Peringia gallica* (Paladilhe 1867) may be referable to this species. The same author's record of *Paludestrina moitessieri* Bourguignat 1876 from Saint-Florent [NN2] may also belong here.

*Hydrobia tetropsoides* (Paladilhe 1870): NM2, NN2 (Mabille 1877, Caziot 1902, Germain 1931; DTH.). Alzona (1971) lists *H. ventrosa* (Montagu 1803) with a query but no details are given and the present form might have been involved. Records of *Peringia obeliscus* (Paladilhe 1869) [Ajaccio—MM4], and *Peringia cyrniaca* J. Mabille 1877 [Portovecchio—NM2] (Caziot 1902, Germain 1931) might also be referable to *H. tetropsoides*.

[*Peringia Mabiliei* (Bourguignat 1876), recorded from near Ajaccio [MM4] (Caziot 1902),



*Paludestrina adjaciensis* (Requien 1848) from Ajaccio [MM4] (Requien 1848, Caziot 1902) and *Paludestrina fagotiana* J. Mabilie in Beringuier 1882 from Bastia, Etang de Biguglia [NN2] and Ajaccio [MM4] (Caziot 1902), are of uncertain identity.]

*Pseudamnicola similis* Germain 1931 *non* (Draparnaud 1805): MM3, MM4, NL1, NM1, NN1, NN2 (Mabilie 1869, Caziot 1902, 1903, Büttner 1926, Germain 1931); The type of *Pseudamnicola similis* (Draparnaud 1805) is reported to be an immature shell of *Bithynia tentaculata* (Linnaeus 1758) so the name is used here in the same sense as by Germain (1931). *P. cyrniaca* (Mabilie 1869) is regarded as a local form of the same species following Germain (1931). The report of '*Amnicola melitensis* Paladilhe 1869' [from NN2] by Caziot (1903) might also have involved this species.

*Pseudamnicola anatina* (Draparnaud 1805): NL1, NM1, NN1, NN2 (Requien 1848, Caziot 1902, 1903, Germain 1931).

*Pseudamnicola lanceolata* (Paladilhe 1869): NL1, NN2 (Caziot 1902, Germain 1931).

[*Amnicola conovula* Parreys 1863: reported from Bonifacio [NL1] by Caziot (1902), is of uncertain identity.]

*Potamopyrgus jenkinsi* (E. A. Smith 1889): MM3, MM4, NM2, NN2 (Doby *et al.* 1966; DTH.). Berner (1963) has recorded the spread of this species in France and Doby *et al.* (1966) and Leger and Leger (1974) give details of its status and spread in Corsica.

*Bythinella opaca* (Frauenfeld 1856): MM3, MM4, NM1, NN2 (Mabilie 1869, Caziot 1902, Büttner 1926, Germain 1931; DTH.); *B. etrusca* (Paladilhe 1867), *B. gaudefroyi* (Mabilie 1869) and *B. ligurica* (Paladilhe 1867) are tentatively regarded as forms of *B. opaca* (cf. Germain 1931, Alzona 1971). Old records of *B. pupoides* (Paladilhe 1869) and *B. abbreviata* (Michaud 1831) are of uncertain status but they could also refer to the present species (cf. Caziot 1902, Germain 1931).

#### Truncatellidae

*Truncatella subcylindrica* (Linnaeus 1758): MM4, MN4, NL1, NM1, NM2, NN2 (Payraudeau 1826, Requien 1848, Caziot 1902; DTH.).

#### Bithyniidae

*Bithynia tentaculata* (Linnaeus 1758): MM4, NN2 (Requien 1848, Caziot 1902; DTH.). '*Bythinia Troscheli* (Paasch 1842)' was listed for Cap Corse [NN1] by Caziot (1902) but the record is more likely of *B. tentaculata* than *B. leachii* (Sheppard 1823), despite the fact that *troscheli* appears to be a form of the latter species.

#### Assimineidae

*Paludinella littorina* (Delle Chiaje 1828): NN2 (Caziot 1902, Germain 1931).

#### Euthyneura

##### Ellobiidae

*Ovatella myosotis* (Draparnaud 1801): NL1, NM1, NN2 (Payraudeau 1826, Shuttleworth 1843, Requien 1848, Caziot 1902; DTH.).

*Ovatella firmini* (Payraudeau 1826): MM4, NL1, NN2 (Payraudeau 1826, Requien 1848, Caziot 1902).

[*Leucophytia micheli* (Mittre 1842): MM4 (Germain 1931 tentatively places the report by Requien 1848 of '? *Auricula Bivonæ* Phil.' here).]

*Carychium minimum* Müller 1774: MM3, NM1, NN2 (Requien 1848, Caziot 1902; DTH.).

*Carychium tridentatum* (Risso 1826): NM1, NN2 (Caziot 1902).

##### Gadiniidae

*Gadinia garnoti* (Payraudeau 1826): MM4 (Payraudeau 1826, Germain 1931).

#### Physidae

[*Physa fontinalis* (Linnaeus 1758) was reported by early authors (Shuttleworth 1843, Requien 1848) but probably in error for *Bulinus* (cf. Caziot 1902, Germain 1931).]



*Physa acuta* Draparnaud 1805: MM4 (DTH.). Older records (Shuttleworth 1843, Requien 1848) may be errors for *Bulinus* (cf. Caziot 1902, Germain 1931).

#### Lymnaeidae

*Lymnaea truncatula* (Müller 1774): MM3, MM4, MN4, NN1, NN2 (Requien 1848, Caziot 1902, Germain 1931; DTH.).

*Lymnaea palustris* (Müller 1774): MM4, MN4, NL1, NM1, NM2, NN2 (Payraudeau 1826, Requien 1848, Caziot 1902, Germain 1931; DTH.).

*Lymnaea peregra* (Müller 1774): MM4, MN4, NL1, NM1, NN1, NN2 (Requien 1848, Mabilie 1869, Caziot 1902, Büttner 1926, Germain 1931; DTH.). ‘*Limnea Aradasi* Caziot 1902’ (ex Bourguignat MS.) is apparently a form of this species. *Lymnaea ovata* Draparnaud 1805 is treated as a separate species by Germain (1931) and Alzona (1971) but I regard it as a form of *L. peregra* following Hubendick (1951).

#### Planorbidae

*Bulinus truncatus* (Audouin 1827): MN4, NN2 (Requien 1848, Caziot 1902, Germain 1931).

*Planorbis planorbis* (Linnaeus 1758): MM3, MM4, NL1, NN2 (Caziot 1902, Germain 1931, Giusti 1976; DTH.); all specimens seen have been of very small size and Giusti (1976) places this form as *Planorbis* cf. *moquini* Requien 1848 (type-locality Corsica). Because of this, records (under various names) of *Gyraulus laevis* (Alder 1838) [from MM4, MN4, NM1, NM2, NN1, NN2] (Requien 1848, Caziot 1902, Büttner 1926, Germain 1931) need confirmation. Old records of ‘*Planorbis carinatus* Müll.’ [NL1, NN2] (Requien 1848) might also be errors, although shells of this species with locality data were in the Draparnaud Collection (Caziot 1902). *Planorbis Brondeli* Raymond 1853, listed by Caziot (1902) for localities in MM4, NL1, NN1 and NN2, may be referable to a small form of *P. planorbis* or to *moquini* if it is a distinct species (see Giusti 1976, pp. 132–143).

*Anisus leucostoma* (Millet 1813): MM4, NM1 (Caziot 1902; DTH.); this species was also recorded without precise locality by Payraudeau (1826). Old records of ‘? *Planorbis acronicus* Fér.’ (Shuttleworth 1843, Requien 1848) could also refer to this species.

*Bathyomphalus contortus* (Linnaeus 1758): MM4 (found by Fabre and listed by Moquin-Tandon, *fide* Caziot 1902).

[*Hippeutis complanatus* (Linnaeus 1758): listed without precise locality by Shuttleworth (1843) and with a question mark [from NN2] by Requien (1848); these old records were doubted by Caziot (1902) and confirmation is needed.]

*Segmentina nitida* (Müller 1774): NN2 (Caziot 1902, Germain 1931).

[*Planorbarius corneus* (Linnaeus 1758): listed by Requien (1848) with a question mark [from NN2]; Caziot (1902) doubts this record.]

#### Ancylidae

*Ancylus fluviatilis* Müller 1774: MM3, MM4, MN4, NL1, NM1, NM2, NN1, NN2 (Requien 1848, Caziot 1902, Büttner 1926, Germain 1931; DTH.). The following forms treated as species by Germain (1931) and others are here regarded as forms of *A. fluviatilis*: *costulatum* Küster 1843, *capuloides* Jan in Porro 1838, *vitaceum* Morelet 1845, *strictum* Morelet 1845 and *riparium* Desmarest 1814.

\**Ferrissia wautieri* (Mirolli 1960): MM4 (DTH.); a single empty shell from mud of dried pool 1 km NE. of Pnte. d’Aspreto near Ajaccio, April 1977.

#### Acroloxidae

[*Acroloxus lacustris* (Linnaeus 1758): recorded without precise locality by Shuttleworth (1843); Requien (1848) gives the locality for Shuttleworth’s record (of a specimen collected by Blauner) as St-Florent [NN2]; Caziot (1902) and Germain (1931) doubt the record.]

#### Succineidae

*Oxyloma* sp.: MM4, MN4, NL1, NM1, NN2 (Requien 1848, Caziot 1902, Büttner 1926,



Germain 1930; DTH.). Although Alzona (1971) and others have reported both *Succinea elegans* Risso (= *O. sarsi* (Esmark 1886)) and *S. pfeifferi* Rossmässler 1835 from Corsica, anatomical study is imperative for accurate determination of species in this genus; my own finds were of immature specimens.

#### Cochlicopidae

†*Hypnophila remyi* (Boettger 1949): NM2, NN2 (Boettger 1949, Giusti 1976, p. 149).

*Cochlicopa lubrica* (Müller 1774): MM3, MM4, NM1, NN2 (Requien 1848, Caziot 1902, Germain 1930; DTH.); Shuttleworth (1843, p. 18) mentions 'einer kleineren Varietät' and Alzona (1971) lists *C. l. exigua* (Menke 1830) for Corsica, both of which could refer to *C. lubricella* (Porro 1838), but there is no definite record of that species.

#### Pyramidulidae

*Pyramidula rupestris* (Draparnaud 1801): NL1, NM1 (Requien 1848, Caziot 1902, Germain 1930).

#### Vertiginidae

\**Columella aspera* Waldén 1966: MM3, NM1 (DTH.). Living specimens collected 3 km N. of Ucciani (350 m) and at Bocognano (600 m) in April 1977 are identical in shell characters to material from Britain (determination confirmed by Dr. C. R. C. Paul). This is the first record of the species from anywhere in southern Europe.

*Truncatellina cylindrica* (Férussac 1807): NM1, NN2 (Caziot 1902; DTH.). My only record is of a single empty shell from 1 km NE. of Tavera, April 1977. Requien's (1848) record of '? *Pupa H. Minutissima* Hartm.' could refer to this species or a congener.

*Vertigo antivertigo* (Draparnaud 1801): MM3, NM1 (DTH.); found living in two sites in April 1977: a swampy riverside fen 3 km N. of Ucciani (350 m) and by a small stream at 1000 m about 4 km SW. of Popolasca. Alzona (1971) lists the species for Corsica but without giving details.

[*Vertigo pygmaea* (Draparnaud 1801): listed [for NN2] by Requien (1848) but this old record (quoted by Caziot 1902, Germain 1930, Alzona 1971) needs confirmation.]

#### Chondrinidae

*Granopupa granum* (Draparnaud 1801): MM4, NL1 (Caziot 1902, Germain 1930).

*Solatopupa guidoni* (Caziot 1903): recorded as *Chondrina similis* (Bruguière) or *C. guidoni* (Caziot 1903) (see Giusti 1976) from: MM1, MM4, MN4, NL1, NM1, NN2 (Requien 1848, Caziot 1902, 1903, Büttner 1926, Germain 1930, Gittenberger 1973).

*Granaria variabilis* (Draparnaud 1801): NL1 (Caziot 1902, Germain 1930, Gittenberger 1973). Old records of *Abida secale* (Draparnaud 1801) from Ajaccio [MM4] are regarded as possible errors by Caziot (1902) and Germain (1930).

#### Pupillidae

[*Pupilla muscorum* (Linnaeus 1758): NN2 (Requien 1848). Although this species is listed for Corsica by Germain (1930) and Alzona (1971) they do not give details and it was not found by Caziot (1902); confirmation of Requien's record seems desirable.]

*Lauria cylindracea* (da Costa 1778): MN4, NL1, NM1, NN2 (Caziot 1902, 1903, Germain 1930; DTH.). Records of '*Pupa umbilicata* Drap.' from the same regions given by Requien (1848) could have also involved the following species.

*Lauria sempronii* (Charpentier 1837): NN2 (Caziot 1902, Germain 1930).

#### Valloniidae

*Vallonia pulchella* (Müller 1774): MM4, NL1, NM1, NN2 (Payraudeau 1826, Requien 1848, Caziot 1902, Germain 1930); most if not all of these records might have included *V. excentrica* Sterki 1892.

*Acanthinula aculeata* (Müller 1774): MM3, MM4, MN4, NM1, NN2 (Caziot 1902, Germain 1930; DTH.).



Enidae

*Ena obscura* (Müller 1774): MN4, NM1, NN2 (Caziot 1902, 1903, Büttner 1926, Germain 1930; DTH.).

*Chondrula tridens* (Müller 1774): NL1 (Caziot 1902, Germain 1930).

*Jaminia quadridens* (Müller 1774): NL1, NM1, NM2, NN2 (Payraudeau 1826, Requier 1848, Caziot 1902, 1911, Germain 1930); Pleistocene fossil in NN2 (Caziot 1911).

[*Zebrina detrita* (Müller 1774): shells in the Melvill-Tomlin Collection at the National Museum of Wales (NMW: 1955: 158. 86.) are labelled 'Bastia, Corsica' [NN2] in Tomlin's handwriting; there is no other record from Corsica, so a mistake in labelling may have been involved.]

Endodontidae

\**Toltecia pusilla* (Lowe 1831): MM3, MM4, NN2 (DTH.); living animals collected from damp low-lying sites in April and December 1977; the shells appear identical to material from southern France. The species is otherwise known from southern France, Macaronesia (Gittenberger *et al.* 1980), Italy (Giusti 1969, 1973) and Sardinia (Alzona 1971). However, nominal taxa from further afield may be conspecific (Gittenberger *et al.* 1980).

\**Punctum pygmaeum* (Draparnaud 1801): MM3, MM4, NM1 (DTH.); found living at five sites, in montane forests and valleys; the shells appear identical to material from France and England.

*Discus rotundatus* (Müller 1774): MM3, MM4, NM1, NM2, NN2 (Requier 1848, Caziot 1902, Büttner 1926, Germain 1930; DTH.).

[*Discus perspectivus* (Muhlfeldt 1816): NN1 (found at Rogliano, Cap Corse by M. Guitton according to Caziot (1902)). Germain (1930) overlooked this reference to a species otherwise unknown in France, but the identity or provenance of the shells may be in doubt.]

Arionidae

*Arion rufus* (Linnaeus 1758): NN2 (Requier 1848). Caziot (1902) and Germain (1930) doubted this record but Quick (1961, p. 147) examined spirit specimens from Corsica.

\**Arion* sp.: MM4 (DTH.); unidentified specimens found 1 km E. of Villanova (NW. of Ajaccio) in December 1977 bore a superficial resemblance to *A. subfuscus* (Draparnaud 1805) but only one immature survived until it could be preserved in spirit.

Vitrinidae

*Phenacolimax annularis* (Studer 1820): MM3, MN4 (Caziot 1902). Caziot (1902, p. 73) also mentions finding a single shell similar to *Vitrina pollonerae* Piero 1896 at Olmi-Cappella [NN2], but the specimen was subsequently broken.

*Vitrina pellucida* (Müller 1774): MM3, MN4, NM1 (Caziot 1902; DTH.); empty shells and living immature animals found at five sites in 1977 (350–1450 m elevation).

Zonitidae

*Zonites algirus* (Linnaeus 1758): NL1, NN2 (Payraudeau 1826, Requier 1848); these records are dismissed by Caziot (1902) and Germain (1930) but they give insufficient reason for this and the species is distinctive.

*Vitrea* spp.: The Mediterranean species of this genus are poorly understood and old records from Corsica have to be regarded with caution. The record of *V. diaphana* (Studer 1820) said to have been collected at Bastia by Blauner quoted by Germain (1930, p. 160) is clearly an error as it is based on misquotation of Shuttleworth (1843); Alzona (1971) also listed this species for Corsica but he may have merely quoted Germain. Germain (1930, p. 161) doubted the identification of specimens possibly of the species now known as *V. subrimata* (Reinhardt 1871) collected by Caziot (1902) on Cap Corse [NN2] although Caziot gives a good description of the tiny umbilicus.

[*V. crystallina* (Müller 1774) has been reported from MM4, NM1 and NN2 (Caziot 1902,



Büttner 1926, Germain 1930, p. 161) but I have not seen Corsican specimens referable to this species and Alzona (1971) may have merely quoted Caziot or Germain.]

[‘*Hyalinia libysonis* Paulucci 1882’ was reported from MN4 by Caziot (1903). Germain (1930) does not list this name, which may be referable to a species of *Vitrea*.]

\**Vitrea contracta* (Westerlund 1871): MM3, MM4, NM1 (DTH.); empty shells and living animals collected in 1977 from six widely separated sites show identical shell characters to material from France, Switzerland and Britain.

\**Vitrea subrimata* (Reinhardt 1871): MM3, NM1 (DTH.); living specimens obtained from two sites in 1977 appear to differ markedly in shell characters from British and Swiss *V. subrimata* in having a much larger umbilicus, but Dr. A. Riedel (*in litt.*) has confirmed that they are similar to other Mediterranean forms of this species.

*Aegopinella pura* (Alder 1830): MN4, NM1 (Caziot 1902; DTH.); living specimens collected from three localities in 1977 (open marsh, beech forest and mixed beech and pine forest; 600–900 m) have shells identical to material from Britain and France (determination confirmed by Dr. A. Riedel).

[*Aegopinella nitens* (Michaud 1831): Caziot (1902) and Germain (1930) wisely doubted the records of ‘*Helix nitens* L. Mich.’ from Ajaccio and Bastia listed by Requien (1848). The identity of *Hyalinia adjaciensis*, described from MM4 by Caziot (1903, p. 34) is uncertain; Germain (1930) overlooked this name which is probably referable to a species of *Aegopinella*.]

\**Oxychilus* (*Ortizius*?) sp.: NM1 (DTH.); living specimens of small Zonitidae referable to this genus were collected at Bocognano (600 m) and in the Forêt de Vizzavona (900 m) in April 1977. Dr. A. Riedel suggests they may represent an undescribed species, but living specimens will need to be collected for anatomical study to allow separation from *Oxychilus perspectivus* (Kobelt), a species known from southern Italy and the Eolie Islands.

[*Oxychilus alliarius* (Miller 1822): reported by Mabille (1869, p. 63), but without precise locality and perhaps in error.]

*Oxychilus glaber* (Rossmässler 1835): NL1, NN2 (Caziot 1902, Germain 1930).

[*Oxychilus cellarius* (Müller 1774): Caziot (1902) and Germain (1930) questioned old records (Payraudeau 1826, Requien 1848) made before many species of the genus had been described.]

*Oxychilus mortilleti* (Pfeiffer 1859): MN4, NL1, NM1 (Caziot 1902, Germain 1930); originally recorded as *O. villae* (Strobel 1853); should perhaps be treated as a southern form of *O. cellarius* (Germain 1930).

*Oxychilus hydatinus* (Rossmässler 1838): reported living and tentatively as a Pleistocene fossil in NN2 (Caziot 1902, 1911, Germain 1930, p. 163).

*Oxychilus draparnaudi* (Beck 1837): MM3, MM4, NM1, NN2 (Caziot 1902, Germain 1930); Requien (1848) reported ‘? *Helix Blauneri*. Shuttlew. Var. *Convexiuscula*’ from Bastia, Corte and Ajaccio but this is probably best dismissed as unidentifiable.

*Oxychilus blauneri* (Shuttleworth 1843): MM4, MN4, NL1, NM1, NM2, NN2 (Requien 1848, Caziot 1902, Büttner 1926, Germain 1930); perhaps only a form of *O. draparnaudi* (Germain 1930).

*Oxychilus obscuratus* (Porro in Villa 1841): MN4, NL1, NM1, NN2 (Caziot 1902, Germain 1930); Pleistocene fossil in NN2 (Caziot 1911); older records have been ignored (Requien 1848, p. 46) because of the risk of misidentifications (cf. Caziot 1911, pp. 241–242).

†*Oxychilus tropidophorus* (Mabille 1969): MM4, MN4, NL1, NM1, NN1, NN2 (Caziot 1902, 1903, Germain 1930; DTH.); Pleistocene fossil in NN2 (Caziot 1911).

[*Oxychilus planella* (Pfeiffer 1853): Germain (1930) questions the reliability of the record of this Italian species from near Ajaccio [MM4] made by Caziot (1902); Alzona (1971) lists the species for Corsica but it is not clear on what basis.]

*Zonitoides nitidus* (Müller 1774): MM4, NN1, NN2 (Caziot 1902, Germain 1930; DTH.); old



records (Payraudeau 1826, Shuttleworth 1843, Requier 1848) have been ignored because it seems likely that several species were confused under this name and some of its synonyms.

# Milacidae

\**Milax nigricans* (Philippi 1836): MM4, NM1 (DTH.); specimens collected from five sites in 1977 were distinguished from the very similar *M. gagates* (Draparnaud 1801) by the presence of conspicuous papillae on the stimulator in the genital atrium (Quick 1961; the name *M. insularis* (Lessona & Pollonera 1882) used by Quick is a synonym of *nigricans*); early authors (Requier 1848, Pollonera 1896, Simroth 1900, Caziot 1902) did not separate *nigricans* and *gagates* so their records (including some from NN2) must be discounted unless specimens can be located.

*Milax rusticus* (Millet 1843): MM4, NM1, NN2 (Pollonera 1896, Simroth 1900, Caziot 1902, Germain 1930; DTH.); the name *Milax marginatus* (Draparnaud 1805) used by Germain (1930) and others is unavailable because *Limax marginatus* Draparnaud 1805 is a homonym of *Limax marginatus* Müller 1774.

*Milax sowerbyi* (Férussac 1823): NN2 (Caziot 1902, Germain 1930).

# Limacidae

*Limax maximus* Linnaeus 1758: MN4, NM1, NN2 (Simroth 1900, Caziot 1902; DTH.); the record by Requier (1848) of '*Limax Cinereus* Mull.' may also refer to this species.

*Limax cinereoniger* Wolf 1803: MM3, NM1 (Caziot 1902, Germain 1930).

*Limax corsicus* Moquin-Tandon 1855: NM1, NM2, NN2 (Caziot 1902, Germain 1930; DTH.).

*Limax flavus* Linnaeus 1758: NN2 (Caziot 1902); Quick (1961, p. 187) examined spirit specimens from Corsica.

*Limax marginatus* Müller 1774: NM1 (Pollonera 1896, Simroth 1900, Caziot 1902, Germain 1930).

\**Limax (Lehmannia) valentianus* Férussac 1821: MM4, NM1 (DTH; specimens identified by Prof. A. Wiktor). This slug is thought to be native to the Iberian Peninsula but it has been introduced by man to many of the warmer parts of the world.

[*Limax* spp.: Simroth (1900) described three new species of this genus from Corsica, *L. wohlberedti*, *L. wolterstorffi* and *L. obscurus*. A detailed revision of this genus in the Mediterranean region is needed to properly assess the status of these names.]

[*Krynockillus cyrniacus* Mabille 1868 is based on such a poor description that it probably cannot be identified even to a genus (Caziot 1902, Germain 1930, p. 105).]

*Deroceras* spp.: This genus is poorly understood in the Mediterranean region and there has been doubt about the validity and application of many names as well as the identification of Corsican forms. I am grateful to Prof. A. Wiktor for identification of my material of this genus.

\**Deroceras laeve* (Müller 1774): MM4, NM1 (DTH.); both aphyallic and euphyallic individuals were found.

\**Deroceras panormitanum* (Lessona & Pollonera 1882): MM4, NM1 (DTH.); this slug has often been known as *D. caruanae* (Pollonera 1891) but *panormitanum* appears to be the valid name (*vide* Prof. A. Wiktor).

[*Deroceras agreste* (Linnaeus 1758): reported as 'assez commun' by Germain (1930) and from a locality in NN2 by Caziot (1902), but perhaps in error for *D. reticulatum*.]

*Deroceras reticulatum* (Müller 1774): MM4, NM1 (DTH.). Alzona (1971) listed this species for Corsica, but it is uncertain on what basis.

†*Deroceras cazioti* (Pollonera 1896): NM1 (Caziot 1902, pp. 66–67, Germain 1930, p. 103; DTH.).

[*Deroceras* spp.: Two nominal species are of uncertain identity, *Agriolimax corsicus* Simroth 1900 (which was described in detail, cf. Germain 1930, pp. 105–106) from Bastia [NN2] and



*Agriolimax sardus* Simroth 1886 (cf. Caziot 1902, p. 67, Germain 1930, p. 106) from Corte [NM1].]

#### Euconulidae

*Euconulus fulvus* (Müller 1774): MM3, NM1 (DTH.); previous authors have not considered the following form to be a separate species, a matter on which evidence is equivocal (cf. Gittenberger, Backhuys & Ripken 1970, Waldén 1976, Kerney & Cameron 1979); the 'aggregate species' was recorded by Shuttleworth (1843, p. 17) and from the environs of Bastia [NN2] by E. Caziot (Caziot 1902, Germain 1930).

\**Euconulus alderi* (Gray 1840): NN2 (DTH.); shells of living animals from the edge of reedswamp at l'Etang de Biguglia collected in December 1977 show all characters of this form.

#### Ferussaciidae

*Ferussacia follicula* (Gmelin 1790): MM4, NL1, NM1 (Requien 1848, Caziot 1902, Germain 1930); some authors consider *F. vescoi* Bourguignat 1856 to be a distinct species (both forms are recorded from all three of the squares listed).

[*Hohenwartia hohenwarti* (Rossmässler 1839): NL1, NN2 (Requien 1848, Caziot 1902, p. 291, 1903, p. 39, Germain 1930); *H. moitessieri* (Bourguignat 1856): NL1 (Caziot 1902, Germain 1930) is sometimes treated as a distinct species. Records of this genus need checking because many of them appear to be based on large shells of *Cecilioides* spp. (M. P. Kerney, pers. comm.).]

*Cecilioides acicula* (Müller 1774): MM4, NL1, NN2 (Requien 1848, Caziot 1902, Germain 1930).

[*Cecilioides liesvillei* (Bourguignat 1856): NN2 (Caziot 1902, Germain 1930); probably only a form of *C. acicula*.]

#### Subulinidae

*Rumina decollata* (Linnaeus 1758): NL1, NM1 (Payraudeau 1826, Requien 1848, Caziot 1902, Germain 1930); reported from Bastia [NN2] by Requien (1848) but Caziot (1902) states that this is an error.

#### Clausiliidae

*Cochlodina laminata* (Montagu 1803): NM1, NN2 (Caziot 1902, Germain 1930). Caziot (*op. cit.*) states that it was introduced.

†*Cochlodina meisneriana* (Shuttleworth 1843): MM3, MM4, MN4, NL1, NM1, NN2 (Shuttleworth 1843, Requien 1848, Caziot 1902, Büttner 1926, Germain 1930, Nordsieck 1969; DTH.); Pleistocene fossil in NN2 (Caziot 1911). Records of *C. kuesteri* (Rossmässler 1836) and *C. porroi* (Pfeiffer 1848) (e.g. Shuttleworth 1843, Requien 1848, Büttner 1926, Alzona 1971) are probably referable to this species (cf. Caziot 1902, Germain 1930, Nordsieck 1969).

*Papillifera papillaris* (Müller 1774): MN4, NL1, NN2 (Requien 1848, Caziot 1902, Germain 1930).

*Papillifera solida* (Draparnaud 1805): NM1 (Requien 1848, Caziot 1902, Germain 1930) and possibly NL1 (Caziot 1902).

[*Clausilia rugosa* Draparnaud 1801: recorded by Payraudeau (1826) from NL1 and NN2 and by Shuttleworth (1843) and Requien (1848), but these records were doubted by Caziot (1902) and confirmation is desirable.]

[*Macrogastera plicatula* (Draparnaud 1801): recorded by Payraudeau (1826) from NL1 and NN2 and by Shuttleworth (1843) and Requien (1848); these records were doubted by Caziot (1902) and confirmation is needed.]

*Balea perversa* (Linnaeus 1758): MM3, MN4, NM1, NN2 (Requien 1848, Caziot 1902; DTH.); *B. deshayesiana* Bourguignat 1860 is regarded as a form of *B. perversa*.



## Testacellidae

*Testacella haliotidea* Draparnaud 1801: NL1, NM2, NN2 (Shuttleworth 1843, Requier 1848, Revelière, *fide* Caziot 1902 and Germain 1930); *T. europaea* de Roissy 1805 is tentatively regarded as a synonym or form of this species.

*Testacella scutulum* Sowerby 1821: MM3, MM4, NM1 (DTH.); Quick (1961, p. 118) examined spirit specimens from Corsica; *Testacella Simoni* Mabilie 1869 is possibly a synonym or form of this species (the type was from NN2) (cf. Caziot 1902, Germain 1930).

## Sphincterochilidae

*Sphincterochila candidissima* (Draparnaud 1801): NL1 (Payraudeau 1826, Requier 1848, Germain 1930; this frequently quoted record is doubted by Caziot 1902).

## Helicidae

*Candidula unifasciata* (Poiret 1801): listed for Bonifacio [NL1] by Requier (1848) but probably in error (Caziot 1902). However, records of *rugosiuscula* Michaud 1831 (NN2: Caziot 1902, 1903, Germain 1930) are presumably this species.

[*Candidula intersecta* (Poiret 1801): listed for Calvi [MN4] by Moquin-Tandon but probably in error (Caziot 1902).]

*Cernuella* (*Cernuella*) *virgata* (da Costa 1778): MM4, MN4, NL1, NM1, NM2, NN1, NN2 (Caziot 1902, 1903, 1908, p. 35, Germain 1930, Alzona 1971; DTH.). Pleistocene fossil in NN2 (Caziot 1911). This variable species has been regarded as including *variabilis* Draparnaud 1801, *maritima* Draparnaud 1805, *xalonica* Servain 1880 and numerous other synonyms listed by Germain (1930), Alzona (1971) and Clerx and Gittenberger (1977).

[*Helix aginnica* Locard 1882 was reported from Bastia [NN2] by Caziot (1902, p. 190). Germain (1930) regarded this form as a synonym of *neglecta* but Clerx and Gittenberger (1977) treat it as a distinct species *Cernuella* (*Cernuella*) *aginnica* (Locard 1882). Because there is no evidence that Caziot examined the genital anatomy of the specimens he reported from Corsica they are best regarded as unidentifiable.]

*Cernuella* (*Xerocincta*) *neglecta* (Draparnaud 1805): MM4, MN4, NL1, NM1, NN2 (Caziot 1902, Germain 1930). *Helicella trepidula* (Servain in Coutagne 1881) is possibly a form of this species (cf. Germain 1930, Alzona 1971, Clerx and Gittenberger 1977, p. 44); it was recorded by Caziot (1902) from Corte [NM1], Bastia [NN2] and Tufa and Piazza on Cap Corse [NN2].

*Cernuella* (*Xeromagna*) *cespitem* (Draparnaud 1801): MN4, NL1, NM1, NN2 (Caziot 1902, 1903; DTH.). Old records of '*H. cespitem* Drap.' (Payraudeau 1826, Shuttleworth 1843, Requier 1848) have been ignored. Caziot's records of *Xeromagna erratica* (Mabilie 1881) are attributed to this species, as also is *X. terverii* (Michaud 1831) (cf. Clerx and Gittenberger 1977) although Caziot (1902, pp. 194–197) regarded Moquin-Tandon's Corsican records of the latter as errors. *Helix Mauryi*, described from NN2 by Caziot (1903, pp. 36–37) may be referable to this species; Germain (1930) apparently overlooked this name.

*Cernuella* (*Microxeromagna*) *vestita* (Rambur 1868): MM4, NM1, NN2 (DTH.); the five records are all from damp grassland beneath 400 m elevation. The type-locality of *Helix vestita* Rambur 1868 was 'In Gallia meridionali, in Corsica et in Hispania' but other authors have overlooked this name or confused specimens with *Helicella conspurcata* (cf. Clerx and Gittenberger 1977, Gasull 1977, Gittenberger and Manga 1977).

[*Cernuella ambielina* (Charpentier 1860): NL1, NN2 (Caziot 1902, Germain 1930); Germain (1930) comments that this is a *nomen nudum* at the reference quoted.]

[*Cernuella acompsia* (Bourguignat 1864): reported from MM4 by Caziot (1903: 36) as *Helix sitifiensis* Bourguignat in Locard 1882; Germain (1930) comments that all French specimens he had seen referred to this species were really *C. variabilis*.]

*Helicella* (*Xerotricha*) *conspurcata* (Draparnaud 1801): MM4, NM1 (DTH.). Records from



MM3, MN4, NL1, NM2 and NN2 (Payraudeau 1826, Requien 1848; Caziot 1902, Germain 1930) could be based on either this species or *Cernuella vestita* (q.v.).

*Trochoidea pyramidata* (Draparnaud 1805): NL1, NN2 (Payraudeau 1826, Shuttleworth 1843, Requien 1848; Caziot 1902 questions these records); listed as very rare on Corsica by Germain (1930) and as present on the island by Alzona (1971).

*Trochoidea trochoides* (Poiret 1789): MM4, NL1, NN2 (Payraudeau 1826, Requien 1848, Caziot 1902, Germain 1930); *T. crenulata* Germain 1930 (*non* Müller 1774) (NL1, NN2) is regarded as a form of *T. trochoides*; *Helicella saint-simoni* listed for Corsica by Alzona (1971) may be *Tropidocochlis Conica*, var. *Saint-Simoni* Caziot 1902, which is a synonym of *T. conica* (Draparnaud 1801) = *T. trochoides* (Poiret 1789).

*Trochoidea elegans* (Gmelin 1791): NL1, NM1, NN2 (Payraudeau 1826, Requien 1848, Caziot 1902, 1903, Büttner 1926, Germain 1930, DTH.); *T. scitula* (Cristofori & Jan 1832) (NM1, NN2) (Caziot 1902, 1903, Germain 1930) is regarded as a form of *T. elegans*.

[*Helicopsis striata* (Müller 1774): recorded by Payraudeau (1826), Shuttleworth (1843) and Requien (1848) [from NL1, NN2] but probably as an error of identification (Caziot 1902).]

*Helicopsis (Xeromicra) apicina* (Lamarck 1822): MN4, NL1, NM1, NM2, NN2 (Requien 1848, Caziot 1902, Germain 1930; DTH.); Pleistocene fossil in NN2 (Caziot 1911).

*Cochlicella conoidea* (Draparnaud 1801): NL1, NN2 (Payraudeau 1826, Requien 1848, Caziot 1902, 1903, p. 218, Germain 1930).

*Cochlicella barbara* (Linnaeus 1758): MM3, MM4, MN4, NL1, NM1, NN2 (Payraudeau 1826, Requien 1848, Caziot 1902, Büttner 1926, Germain 1930; DTH); the name *Cochlicella ventricosa* (Draparnaud 1801) has been replaced by *C. barbara* (Linnaeus 1758).

*Cochlicella acuta* (Müller 1774): MN4, NL1, NM1, NM2, NN1, NN2 (Payraudeau 1826, Requien 1848, Caziot 1902, 1908, p. 35, Germain 1930, Lanza 1972; DTH.).

[Caziot (1902) lists a number of Helicellinae of uncertain identity which were apparently overlooked by Germain (1930):

*Helix tacapica* Letourneux & Bourguignat 1885: Bonifacio [NL1];

*Helix krizensis* Bourguignat 1887: near Bonifacio [NL1];

*Helix albovariegata* Caziot 1902, pp. 174–176: Bonifacio [NL1];

*Helix odarsensis* P. Fagot 1883: near Bastia [NN2];

*Helix scita* Caziot 1902, pp. 178–180: Bonifacio [NL1];

*Helix limara* Bourguignat in Locard 1882: Bastia [NN2];

*Helix marsylliana* J. Mabilie 1881: Bastia [NN2];

*Tropidocochlis contermina* Caziot 1902: pp. 217–218 (ex Shuttleworth MS.): Bonifacio [NL1]; listed for Corsica as *Helicella contermina* by Alzona (1971).]

[*Helix vetabola* Westerlund 1889: was listed for NN2 by Caziot (1903, p. 38) and overlooked by Germain (1930); its identity is uncertain.]

[*Helix tartagiana* Caziot 1902 pp. 182–184 (cf. Caziot 1903, p. 33): Pioggiola (Tartagine) [MN4] is probably unidentifiable (Germain 1930, cf. Alzona 1971).]

*Monacha cantiana* (Montagu 1803): MM3, MN4, NL1, NM1, NN2 (Requien 1848, Caziot 1902, 1903, Büttner 1926, Germain 1930); Pleistocene fossil in NN2 (Caziot 1911). Some confusion in interpreting synonymies has arisen in the past because *Helix cartusiana* Draparnaud 1801 = *M. cemenalea* (Risso 1826) not *H. cartusiana* Müller 1774. *M. cemenalea* (of which *M. bastitensis* (Caziot 1902) is a synonym, *fide* Germain 1930, cf. Büttner 1926, Alzona 1971) is regarded as a form of *M. cantiana* (cf. Germain 1930, Alzona 1971).

*Monacha cartusiana* (Müller 1774): MM4, MN4, NL1, NM1, NN2 (Requien 1848, Caziot 1902, 1903); listed for Corsica by Germain (1930) and Alzona (1971).

†*Monacha corsica* (Shuttleworth 1843): MM3, MM4, NL1, NM1, NM2, NN2 (Shuttleworth 1843, Requien 1848, Caziot 1902, Germain 1930; DTH.).

†*Monacha perlevis* (Shuttleworth 1852): MM4, MN4, NM1, NN2 (Shuttleworth 1852, Caziot 1902, Germain 1930). F. Giusti (*in litt.*) is currently reexamining the status of this and other



Corsican *Monacha*.

[*Helix astenia* [J. Mabilie] Caziot 1902 is of uncertain identity. It is said to be based on a specimen from Corsica (Caziot 1902, p. 92); Germain (1930) apparently overlooked this name.]

*Hygromia cinctella* (Draparnaud 1801): NL1, NN2 (Payraudeau 1826, Requier 1848, Caziot 1902, Germain 1930).

*Perforatella glabella* (Draparnaud 1801): NN2 (Caziot 1902).

[*Trichia hispida* (Linnaeus 1758): living at Bonifacio [NL1] (Romagnoli, *vide* Caziot 1902); Pleistocene fossil in NN2 (Caziot 1911); these identifications may be in need of confirmation.]

*Caracollina lenticula* (Michaud 1831): MM4, MN4, NL1, NM1 (Requier 1848, Caziot 1902, Germain 1930).

[*Chilostoma squamatum* (Moquin-Tandon 1856): old records of *Helix cornea* Draparnaud from Bonifacio (Payraudeau 1826, Shuttleworth 1843, Requier 1848) are presumably attributable to species of *Tachycampylaea* or *Marmorana* (cf. Caziot 1902). The familiar name *Helix cornea* Draparnaud 1801 has been replaced because it is preoccupied by *Helix cornea* Linnaeus 1758.]

*Marmorana serpentina* (Férussac 1821): MN4, NL1, NM2, NN1, NN2 (Payraudeau 1826, Requier 1848, Caziot 1902, 1903, 1916b, Büttner 1926, Germain 1930, Lanza 1972); Pleistocene fossil from NN2 (Caziot 1911). Following de Bartolomé (1981), *M. suburbana* (Paulucci 1882) (NL1) and other named forms are treated as conspecific with *M. serpentina*.

†*Tachycampylaea raspaili* (Payraudeau 1826): MN4, NM1, NM2, NN2 (Payraudeau 1826, Requier 1848, Mabilie 1869, Hagenmüller 1888, Caziot 1902, 1903, 1916a, Büttner 1926, Germain 1930); Pleistocene fossil in NN2 (Caziot 1911, 1916a, 1917); the complex synonymy of this species and its congeners is listed by Hagenmüller (1888) and Germain (1930).

†*Tachycampylaea insularis* (Crosse & Debeaux 1869): NM1, NN2 (Crosse and Debeaux 1869, Caziot 1902, 1916a, Germain 1930); Pleistocene fossil in NN2 (Caziot 1911, Germain 1930). This may only be a form of *T. raspaili* (cf. Germain 1930) although Caziot (1902) points out some anatomical differences.

†*Tachycampylaea brocardi* (Dutailly 1867): MN4, NL1, NM1, NN2 (Dutailly 1867, Mabilie 1869, Hagenmüller 1888, Caziot 1902, 1916a, Germain 1930), Pleistocene fossil in NN2 (Caziot 1911, Germain 1930).

†*Tachycampylaea revelierei* (Debeaux 1867): NL1, NM1, NN2 (Payraudeau 1826, Requier 1848, Hagenmüller 1888, Caziot 1902, 1916a, Germain 1930).

†*Tachycampylaea romagnoli* (Dutailly 1867): MN4, NM1 (Dutailly 1867, Hagenmüller 1888, Caziot 1902, 1916a, Germain 1928, 1930).

[*Tachycampylaea carotii* (Paulucci 1882): reported from NM1 (Caziot 1902, p. 141, cited by Germain 1930, pp. 206–207); however, Caziot (1916a) states that this was an error of identification.]

[*Tachycampylaea venacensis* (Pollonera in Caziot 1902): NM1 (Caziot 1902 p. 142, 1916a, Germain 1930); Pleistocene fossil in NN2 (Caziot 1911, p. 244, Germain 1930), Germain (1930, p. 207) comments that this may be a form of *T. carotii*.]

[*Tachycampylaea arusalensis* (Hagenmüller 1888): NM1, NM2 (Hagenmüller 1888, pp. 47–49, Caziot 1902, p. 137, 1916a, Germain 1930); the taxonomic status of this form is dubious.]

[*Pseudotachea splendida* (Draparnaud 1801) and *Cepaea nemoralis* (Linnaeus 1758) were listed by early authors (Payraudeau 1826, Shuttleworth 1843, Requier 1848) but probably in error (Caziot 1902, Germain 1930); confusion with species of *Tachycampylaea* or *Marmorana* seems likely.]

*Theba pisana* (Müller 1774): MM4, MN4, NL1, NM1, NN2 (Payraudeau 1826, Shuttleworth 1843, Requier 1848, Caziot 1902, Germain 1930).

*Eobania vermiculata* (Müller 1774): MM4, MN4, NL1, NM1, NN1, NN2 (Payraudeau 1826, Requier 1848, Caziot 1902, 1908, p. 35, Germain 1930; DTH.); Pleistocene fossil in NN2



(Caziot 1911).

*Otala lactea* (Müller 1774): NN1, NN2 (Requien 1848, Caziot 1902, Germain 1930).

*Helix aspersa* Müller 1774: MM4, NL1, NM1, NN2 (Requien 1848, Caziot 1902, Büttner 1926; DTH.); Pleistocene fossil in NN2 (Caziot 1911). *Helix aggerivaga* J. Mabilie 1880, said to be from Corsica, is probably referable to this species (cf. Caziot 1902, p. 243).

[*Helix melanostoma* Draparnaud 1801: old records (Payraudeau 1826, Shuttleworth 1843, Requien 1848) are dismissed by Caziot (1902) and Germain (1930), presumably because of the absence of recent records and the possibility of confusion with one or another of the following species. However, Caziot (1903, p. 39) quotes at second-hand a report of what was apparently a Pleistocene fossil found by Debeaux [in NN2].]

*Helix aperta* Born 1778: MM3, MM4, MN4, NL1, NM1, NN2 (Payraudeau 1826, Requien 1848, Caziot 1902, Büttner 1926; DTH.); Pleistocene fossil in NN2 (Caziot 1911).

†*Helix ceratina* Shuttleworth 1843: MM4 (Shuttleworth 1843, Requien 1848, Lecoq 1851, Caziot 1902, Germain 1930). Recent empty shells were found in 1974 (J. F. M. de Bartolomé, pers. comm.). Requien (1848, p. 44) and all subsequent authors have adopted the name *Helix tristis* Pfeiffer 1845 for this species, despite the evident availability and priority of Shuttleworth's name; Caziot (1902) thought *ceratina* was a *nomen nudum* but Shuttleworth gives a short diagnostic description; as little confusion can arise through application of strict priority in this instance I have reverted to using the senior name.

[*Helix nuculoides* Caziot 1911: Pleistocene fossil in NN2 (Caziot 1911 pp. 240, 243–244, Fig. 3); this nominal species has been widely overlooked; it may well be a synonym of *H. aperta* or *H. ceratina*.]

[‘*Helix leucozona* Ziegler’: Pleistocene fossil in NN2 (Caziot 1903 p. 39, 1911 p. 245); these references were overlooked by Germain (1930); however, the identification may be questioned.]

## Bivalvia

### Unionidae

†*Unio turtoni* Payraudeau 1826: MM3, MM4, NM1, NM2 (Payraudeau 1826, Requien 1848, Caziot 1902, Germain 1931); *Unio capigliolo* Payraudeau 1826 is tentatively regarded as a synonym because the two forms generally occur together and Caziot (1902) reports numerous intermediates. Further study may show these mussels to be forms of *Unio crassus* Philipsson 1788 or some other continental species.

### Sphaeriidae.

*Sphaerium lacustre* (Müller 1774): NL1, NN2 (Requien 1848, Germain 1931); Caziot (1902) doubts the record from Bastia [NN2].

[*Pisidium amnicum* (Müller 1774): was reported from Bastia [NN2] by Requien (1848) but perhaps in error (Caziot 1902).]

*Pisidium casertanum* (Poli 1791): MM3, MM4, NM1, NN2 (Requien 1848, Caziot 1902, Germain 1931; DTH.).

\**Pisidium personatum* Malm 1855: MM4, NM1 (DTH); found living in small stream at 1000 m elevation 4 km SW. of Popolasca and in small stream at 200 m elevation 1 km E. of Villanova (NW. of Ajaccio).

*Pisidium obtusale* (Lamarck 1818): MM4, NN2 (Caziot 1902, Büttner 1926, Germain 1931); Requien (1848) records it from Bonifacio (NL1) but such an old identification must remain suspect for *Pisidium*; Ellis (1962, p. 48) records the species for Corsica.

*Pisidium nitidum* Jenyns 1832: NM1 (Caziot 1902, Germain 1931); Ellis (1962, p. 60) records the species for Corsica; ‘*Pisidium pusillum* Gmelin’ recorded from NN1 and NN2 by Caziot (1902) and from MM3 by Büttner (1926) could have been this species but the name given is ambiguous.



[*Pisidium pulchellum* Jenyns 1832: NN2 (Caziot 1902), also listed for Bonifacio [NL1] by Requier (1848); both of these old records need confirmation.]

[*Pisidium milium* Held 1836: NN2 (Caziot 1902, as *P. gassiesianum* Dupuy 1849, but Germain 1931 considers this record doubtful).]

[*Pisidium planulatum* Baudon 1857: recorded from Cap Corse [NN1, NN2] by Caziot (1902), is of uncertain identity.]

## ACKNOWLEDGEMENTS

I am grateful to Monsieur Jean-Claude Thibault for hospitality on successive visits to Corsica and for assistance with fieldwork. Thanks are due to Mr. J. F. M. de Bartolomé for information on Helicidae, Prof. F. Giusti for checking certain identifications, Dr. C. R. C. Paul for checking *Columella*, Dr. A. Riedel for checking and identifying Zonitidae and to Prof. A. Wiktor for identifying the Limacidae. Dr. B. Coles, Dr. E. Gittenberger, Prof. F. Giusti and Dr. M. P. Kerney made helpful comments on my manuscript.

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N.V.=original not verified.

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## HOLYOAK: DISTRIBUTION OF LAND AND FRESHWATER MOLLUSCA IN CORSICA

## APPENDIX

Principal collections of land and freshwater Mollusca from Corsica.

<i>Years</i>	<i>Collector</i>	<i>Publications</i>	<i>Location of Specimens</i>
1824–5	B.-C. Payraudeau	Payraudeau (1826)	Muséum National d'Histoire Naturelle, Paris
1842	Herr Blauner	Shuttleworth (1843)	Naturhistorischen Museum, Bern
1822, 1847	E. Requien ( <i>et al.</i> )	Requien (1848)	Avignon? Ajaccio?
1865–70	MM. Debeaux, Locard		Lyon?
1867–80	P. Mabille	J. Mabille (1877)	?
1885, 1887	P. Hagenmüller	Hagenmüller (1888)	Marseille?
1899	Herr Wolterstorff	Simroth (1900)	Senckenberg-Museums, Frankfurt a. M.
c. 1895–1906	E. Caziot (with MM. Maury, Guiton, <i>et al.</i> )	Caziot (1902, 1903, etc.), Polonéra (1896)	Nice?
1914	Dr. P. Schottländer—Expedition	Büttner (1926)	Museum für Naturkunde, Berlin (east)
1948	Dr. P. Remy	Boettger (1949)	Laboratoire de Zoologie, Faculté des Sciences, Nancy & Senckenberg-Museums, Frankfurt a. M.
1956–80	J. F. M. de Bartolomé	de Bartolomé (1981)	Colln. J. F. M. de Bartolomé
1971, 1972	B. Lanza	Lanza (1972)	Istituto di Zoologia, Università di Siena
1977	D. T. Holyoak	this paper	Colln. D. T. Holyoak
1978,	Prof. F. Giusti	in prep.	Siena, Italy



# PROCEEDINGS OF THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

## REPORT OF THE COUNCIL 1982–1983

It is with regret that the Society has to report the deaths of the following 5 members; Mr. R. B. Jansen who joined in 1937, Prof. H. P. Moon who joined in 1971, Mr. F. G. Wagner who joined in 1981, Miss B. Temple who joined in 1968, and Mr. A. E. Ellis, who joined in 1923, and was an Honorary member of the Society and a past President.

The total membership of the Society now stands at 633 and is comprised of the following categories:—  
Full members 520, Full life members 35, Family members 41, Family life members 7, Honorary members 4, Junior members 26, total 633. *Resignations* Full members 23, Junior members 5, total 28. *Struck off for non-payment of subscription* Full members 17, Junior members 6. total 23.

### *New members nominated & elected during 1982/83*

Full members 46, Family members 10 Junior members 8, total 64. 2 junior members transferred to full membership.

### *Subscribers*

The total number of subscribers is 153 to the *Journal of Conchology* (after 3 cancellations), and 11 subscribers to the *Conchologists' Newsletter* and *Papers for Students*.

### *Meetings*

There were 7 ordinary meetings held in the Demonstration room of the British Museum (Natural History), together with one Annual General Meeting and Special General Meeting.

### *Publications*

Two parts of the *Journal of Conchology* were issued (Volume 31, parts 1 & 2). Four issues of *The Conchologists Newsletter* were printed and issued with the Annual Programme card of events. An updated list of changes in the membership was issued instead of the usual full list of members as an economy measure in view of the high cost of printing. No papers for students were issued.

### *Field Meetings 1982*

Nine field meetings were held during 1982 as follows:—

2nd. May, Bexhill, East Sussex. 22nd. May, Ipswich, Suffolk. 30th. May, Luton, Beds. 6th. June, Joint meeting with the Northampton N.H.S. 19th.–28th. June, Isle of Skye. 18th. July, Bedfordshire. 24th. July, Sandwich, Kent. 18th. Sept., Ketton, Rutland. 17th. Oct., Burnham Beeches, Bucks.

Thanks are due to the following for leading these meetings:— Mrs. C. J. Pain, Mrs. E. B. Rands and Messrs I. M. Evans, I. J. Killeen, A. P. H. Oliver, A. G. H. Osborn, D. G. Rands and D. R. Worth.

J. D. NUNN, HON. SECRETARY

## TREASURER'S REPORT, 1982

The Society's finances appear in a healthy condition at present. This arises to some extent from the decrease in the rate of inflation, which was considerably more than had been expected. In addition the increase in Subscriptions has produced an increased income, and the year has shown a large increase in sales of publications and a substantial rise in donations; there has also been a slight increase in the investment income.

Three of the Society's investments reached the end of their term. The Mersey Docks and Harbour Board Loan Stock, 1980/82, was repaid. The Trustees arranged advantageous renewals for the City of Norwich 12½% Loan (renewed at 14½%) and the Borough of Bury 12¼% Loan (renewed at 13%).

Although several *Papers for Students* are in preparation none were available for publication in 1982, but your Council took the opportunity of purchasing a stock of paper for printing them at a reasonable price.

Additional Members have covenanted their Subscriptions, and the Society is grateful to all covenanted Members for the useful sum of £247.35.



THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

# INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31st DECEMBER 1982

Publications:—				Fees and Subscriptions:—				PROCEEDINGS	
News Letter	...	...	2,356.25	Membership Fees	...	...	5,354.36		
Student Papers	...	...	196.30	Subscriptions	...	...	3,050.35		
				Entrance Fees	...	...	52.00	8,456.71	
Journal:—									
Volume 31 No. 1	...	...	3,084.54	Donations				342.24	
Volume 31 No. 2	...	...	2,259.57						
Cover for Volume 31	...	...	430.00						
Sealing Permit	...	...	20.00	Sales:—					
			5,794.11	Atlas	...	...	52.79		
				Advertising	...	...	83.50		
				Journals	...	...	252.00		
Printing, Stationary and Postage	...	...	671.74	Student Papers	...	...	92.40		
Postage and Packing	...	...	217.00	News Letter	...	...	69.04		
Officers Expenses	...	...	334.06	Shell Kits	...	...	30.00		
Meetings	...	...	180.00	Book Markers	...	...	5.00		
Subscriptions	...	...	7.00	Sundries	...	...	30.00	614.73	
				Special Publication				119.50	
				Investment Income:—					
				General Account	...	...	1,084.38		
				Life Members Fund	...	...	430.46		
				Reserve and Research Fund	...	...	266.83		
				Transfer to Reserve and					
				Research Fund	...	...	266.83		
Net Surplus	...	...	1,291.56					1,514.84	
			£11,048.02					£11,048.02	



BALANCE SHEET AS AT 31st DECEMBER 1982

Creditors and Accrued Charges	...	1,343.21	Cash at Bank:—		
			Current Account	...	1,222.68
Fees and Subscriptions in Advance		1,408.30	Deposit Account	...	2,813.46
Life Membership Fund	...	2,890.00	Post Office Savings Bank	...	4,483.01
					8,519.15
Reserve and Research Fund	...	2,058.21	Investments:—		
			£400 5% Treasury Stock 1986/89		344.00
			2514 Units M. & G. Dividend Fund		1,522.06
			£400 14½ Loan—City of Norwich		400.00
			£800 5½% Loan—London County Council	...	769.20
			1620 Save and Prosper Units	...	892.95
			£875 Spillers 7% Debenture Stock 1978/83	...	753.82
			£700 Bury—13% Loan	...	700.00
			£800 15½% Treasury Stock 1998	...	768.00
Balance Brought Forward	...	7,280.25	£93.60 Subordinated Loan Stock—Mersey Docks & Harbour Board		93.60
Add Surplus for the Year	...	1,291.56	104 10p Ordinary Shares—Mersey Docks & Harbour Board	...	10.40
			£2340 7¼% Whitbread Stock 1995/99		1,498.38
					7,752.41
					£16,271.56

WM. F. EDWARDS }  
L. LLOYD-EVANS } *Hon. Auditors*

MARJORIE FOGAN  
*Hon. Treasurer*

1st March, 1983



## PROCEEDINGS

27 Ordinary Members and 1 Junior Member are in arrears with 1982 Subscriptions. No further publications can be sent in 1983 to any Member whose current Subscription remains unpaid, although these will be sent upon receipt of arrears.

The position regarding banker's orders continues to cause concern. May I urge all Members paying their Subscriptions by banker's order to check that the amount is correct (it is always possible—indeed, it has happened—that the bank has failed to act upon an amended order) and to forward any amount outstanding. Several Members have failed to amend their orders since 1979, and quite a large number did not do so in 1982. This state of affairs is most unsatisfactory, and I appeal to Members to make the necessary adjustments.

MARJORIE FOGAN, HON. TREASURER.

## RECORDER'S REPORT: NON-MARINE MOLLUSCA

The following new vice-comital records have been verified since the last Report (*J. Conch., Lond.* **31**: 132). Unless stated otherwise, the specimens were collected in 1982–3. All the Irish records were made by a Conchological Society mapping party in April 1982 (R. Anderson, Mrs M. Fogan, D. T. Holyoak, R. C. Preece, Mrs E. B. Rands, Mrs H. C. G. Ross, Miss M. B. Seddon).

- Devon South (3): *Leiostyla anglica*, Loddiswell (20/7348), B. Colville.  
Kent East (15): *Perforatella rubiginosa*, Aylesford (51/7358), E. G. Philp.  
Hertford (20): *Boettgerilla pallens*, Tring (42/9511), A. G. H. Osborn.  
Middlesex (21): *Perforatella rubiginosa*, Syon Marshes (51/1776), B. Verdcourt.  
Oxford (23): *Perforatella rubiginosa*, South Stoke (41/5983), F. Naggs.  
Suffolk West (26): *Milax gagates*, Old Newton (62/0462), I. J. Killeen.  
Stafford (39): *Leiostyla anglica*, Brierley Hill (32/9387), P. Tattersfield.  
Leicester (55): *Pupilla muscorum*, Tickencote (43/9809), A. J. Rundle.  
Aberdeen North (93): *Vertigo substriata*, *Acanthinula aculeata*, *Zenobiella subrufescens*, Cright Wood (38/8239), Mrs D. K. Marriott, 1981.  
Main Argyll (98): *Hippeutis complanatus*, Connel (17/9331), Mrs D. K. Marriott.  
Ross East (106): *Vallonia excentrica*, Redcastle (28/5850), R. C. Preece.  
Tipperary South (H7): *Arion fasciatus*, Ballinure crossroads (21/1545).  
Clare (H9): *Hydrobia ventrosa* seg., Lough Murree (12/2511); *Bithynia leachii*, R. Shannon, O'Brien's Bridge (11/6666).  
Wexford (H12): *Hydrobia ventrosa* seg., Tacumshin Lake (31/0304).  
Meath (H22): *Arion fasciatus*, *Milax gagates*, Tullaghanstown (22/7965).  
Westmeath (H23): *Milax gagates*, Littleton House (22/0952).  
Longford (H24): *Milax sowerbyi*, *M. budapestensis*, Scally's Bridge (22/2260); *Limax marginatus*, Dring (22/3185); *Deroceras caruanae*, Gortymone Lough (22/2297); *Cepaea hortensis*, Gowna (22/3289); *Pisidium pseudosphaerium*, Royal Canal, Scally's Bridge (22/2260).  
Leitrim (H29): *Arion 'lusitanicus'*, sensu Quick, Carrigallen (23/2303); *Anodonta anatina*, Lough Erril (22/0497); *Pisidium henslowanum*, Greenagh Lough (22/1096).  
Cavan (H30): *Vallonia excentrica*, Rathkenny House (23/5311); *Acanthinula aculeata*, Killycluggin (23/2416); *Ena obscura*, Nadreegee Lough (22/5293); *Arion fasciatus*, Bellanagh (22/3898); *Milax gagates*, Killinkere (22/6193); *Limax maculatus*, Kingscourt (22/7797); *Deroceras caruanae*, *Cepaea hortensis*, Aghadreenagh (22/5199).  
Louth (H31): *Deroceras caruanae*, Port (32/1589).  
Monaghan (H32): *Potamopyrgus jenkinsi*, Long Lough (23/5717); *Acicula fusca*, *Milax sowerbyi*, *M. budapestensis*, *Limax maculatus*, *Deroceras caruanae*, 5 miles S. of Monaghan (23/6729); *Vertigo lilljeborgii*, Knockaturly Lochan (23/6729); *Cepaea hortensis*, Lisnalong (23/6616).

This year has seen a further species added to the British list: the continental helcid *Perforatella rubiginosa* (Schmidt). A full account of its discovery at Syon Marshes on the River Thames opposite Kew Gardens is given by Dr Verdcourt in *Conchologist's Newsletter* no. 83, p. 46. The species was subsequently found living in similar places by the Thames in Oxfordshire and by the Medway in Kent. The shell of *P. rubiginosa* strongly resembles that of *Trichia plebeia* and the species has no doubt been overlooked for that reason. Any '*plebeia*' from likely habitats (marshy ground on river floodplains) should be examined carefully, preferably by dissection, as the anatomy is quite distinct (see Naggs, *J. Conch. Lond.* **31** (1983) pp. 201–206).

M. P. KERNEY, NON-MARINE RECORDER







# COMMUNICATIONS

## VERTIGO ANGUSTIOR JEFFREYS LIVING IN SUFFOLK

On 3 April 1982, in company with Mr J. M. Gobbitt, I found *Vertigo angustior* living at Martlesham Creek, a small tidal inlet on the northern side of the estuary of the R. Deben, East Suffolk (v.c. 25). The site is about half way along the southern side of the creek (TM 264472).

The vegetation shows a clear zonation down to the water's edge, as follows:

1. hedgerow with *Quercus robur* L.
2. zone of tall herbs *ca* 10 m wide (height 1–2 m). Present in order of decreasing abundance were *Pteridium aquilinum* (L.), *Rubus fruticosus* agg., *Convolvulus arvensis* L., *Calystegia sepium* (L.), *Poa* spp., *Urtica dioica* L., *Epilobium hirsutum* L., *Galium aparine* L., *Phalaris arundinacea* L.
3. zone *ca* 10 m wide dominated by *Carex riparia* Curt., about 1 m tall on the inland edge but lower and more patchy below. Also present in smaller quantities were *Iris pseudacorus* L. (inland edge only), *Calystegia sepium*, *Galium aparine*, *Lycopus europaeus* L., *Urtica dioica*, *Rubus fruticosus* agg., *Poa pratensis* L., *Cirsium arvense* (L.) and *Phalaris arundinacea*.
4. drift-line deposits 3–4 m wide composed mainly of stems of *Phragmites australis* (Cav.), accompanied by such flotsam as wood, bottles, etc.
5. zone of salt-marsh vegetation *ca* 20 m wide growing on mud; species include *Triglochin maritima* L., *Puccinellia* spp., *Atriplex* spp., *Scirpus maritimus* L., *Juncus gerardii* Lois. and *Festuca rubra* L.

*Vertigo angustior* and *V. pusilla* were found only in zone (3), on leaf litter and decaying vegetation at the base of sedges. Both were uncommon, only 26 specimens (17 *V. angustior*, 9 *V. pusilla*) being collected on two visits by field searching and by the sieving of about five litres of dried litter. The associated Mollusca were *Carychium minimum*, *Cochlicopa lubrica*, *Vertigo pygmaea*, *Punctum pygmaeum*, *Discus rotundatus*, *Arion ater* agg., *Oxychilus alliarius*, *Euconulus alderi*, *E. fulvus*, *Clausilia bidentata*, *Trichia hispida* and *Arianta arbustorum*.

Both *Vertigo pusilla* and *V. angustior* are rare in the eastern counties, indeed *V. angustior* is very rare nationally in Britain. There are two old records only for *V. angustior* in Suffolk: Redgrave Fen (Mayfield, *J. Conch.*, *Lond.* **12** (1909), p. 277) and Aldeburgh (Cooper, *J. Conch.*, *Lond.* **8** (1896), p. 171). Cooper's specimens are in the BMNH and have been examined by Dr M. P. Kerney, who states that they are fresh and were obviously collected live (*pers. comm.*). The exact location of the site is unknown, though Aldeburgh does lie on a tidal river (the Alde) and it is therefore possible that Cooper's specimens were collected from a habitat similar to that at Martlesham Creek.

The Martlesham Creek site is unusual in Britain for its apparent association of these two *Vertigo* species. *V. angustior* is normally found in rich marshy grassland, or in wet mossy hollows in sand dunes, whereas *V. pusilla* normally requires drier habitats: rocks, stone walls, open woodland. They are, however, sometimes associated abroad. For example, Waldén records them living together in southern Sweden, where they occur in moist woodland on talus and boulder slopes (*J. Conch.*, *Lond.* **30**, p. 351). In English Postglacial deposits the two species are commonly associated, for example in tufa deposits in Suffolk at Chantry and in the Fynn valley, both near Ipswich, where they occur with *Vertigo substriata* and other Mollusca indicative of wet open woodland.

I should like to thank Dr D. T. Holyoak for examining the vegetation at the site, Dr M. P. Kerney for confirming the identity of *Vertigo angustior* and *V. pusilla*, and Dr R. C. Preece for assistance with fossil material.

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## DORMANCY IN LYMNAEA

Specimens of *Lymnaea peregra* (Müller), recovered from temporary habitats in East Yorkshire possess a pattern of behaviour whereby the snail rotates its foot and applies it to the inside of the shell, so that the side of the body, rather than the foot, occludes the aperture. Such behaviour has been shown to reduce evaporative water loss and was presumed to be 'of adaptive value' to the species (Storey, *J. Conch. Lond.* **27** (1972) p. 377).

When subjected to drying out, under controlled laboratory conditions, juveniles of *Lymnaea truncatula* (Müller), *L. stagnalis* (L.) and *L. palustris* (Müller) adopt the same posture as had previously been described for *L. peregra* only. Although it is easy to see the advantage of such behaviour in species consistently inhabiting areas that dry up, i.e. *L. peregra* and *L. truncatula* in the River Hull, (R. Storey, Ph.D. Thesis, Open University (1982)) and elsewhere (Boycott, *J. Anim. Ecol.* **5** (1936) pp. 116–186), its value is less obvious in species such as *L. stagnalis* which occurs in large bodies of water and is unlikely, therefore, ever to experience desiccation.



It seems probable that the 'adaptive value' of the behaviour described is not really an adaptation at all, in the true sense. There are several examples of organisms from flowing water and from elsewhere whose structure has been accorded the status of 'adaptation', when it was, in fact, merely characteristic of their taxonomic group (H. B. N. Hynes, *The ecology of running water*, Liverpool Univ. Press (1970) pp. 121–160). In their phylogeny, the aquatic pulmonates are described by Russell-Hunter (*Pulmonates*, (Vol. 2A) Eds. V. Fretter and J. Peake, Academic Press (1978) pp. 345–6) as representing a sequence of readaptation to aquatic life. Because the attribute described in this note is possessed by all four species considered, irrespective of habitat, it seems likely that such behaviour is more probably a vestige of their terrestrial ancestry, rather than an adaptation specific to those species inhabiting temporary bodies of water. This explanation suggests that *Lymnaea* as a group may have progressed less far than other pulmonates along the path to aquatic readaptation.

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## NEW NAMES FOR SUBSPECIES OF *GULELLA*

A new name is required for a subspecies of *Gulella* (Pulmonata, Streptaxidae) which I described in 1970 the name having been employed by Germain for a species almost 50 years ago. The only excuse I can give for this piece of carelessness is that the Botanical and Zoological Rules are different (as I well know)—under the former, names compete strictly within their own rank whereas in the latter they compete within a group of species and subspecies names.

### ***Gulella ugandensis brathayi* nom. nov.**

*G. ugandensis cheranganiensis* Verdcourt in *Basteria* **34** (1970) p. 49 non *G. cheranganiensis* Germain (1934).

The new epithet, commemorates the Brathay Exploration Group under whose aegis the expedition to the Cherangani Hills took place, on which I. Thomas collected the original material.

A new name is also required for another subspecies for a similar reason although in this case both the competing epithets are my own; one was described at varietal rank in 1956 so that the name is available, the other in 1965 as a subspecies so that the name merely needs replacing.

### ***Gulella conradti reductidentata* Verdcourt; Zilch in *Arch. Moll.* **90** (1961) p. 93, taf. 6 fig. 33.**

*G. conradti* (von Marts.) var. *reductidentata* Verdcourt in *Proc. malac. Soc. Lond.* **32** (1956) p. 69, fig. 3, 3a.

### ***Gulella planidens wilkinsoni* nom. nov.**

*G. planidens reductidentata* Verdcourt in *Arch. Moll.* **94** (1965) p. 165, fig. 1.

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## *LAURIA SEMPRONII* FROM A NEOLITHIC FLINT MINE IN SUSSEX

The small pupillid *Lauria sempronii* (Charpentier) has been reported as a fossil from three places in S.E. England (*J. Conch., Lond.* **24** (1957), p. 183), and was found living ninety years ago at one locality in Gloucestershire (*J. Conch., Lond.* **27** (1972), p. 517). In view of the essentially alpine and south European distribution of this species its presence in Britain is something of a puzzle. Two of its fossil occurrences are from chalky slope deposits on the North Downs, of uncertain but late Postglacial age. The third (a single shell) came from excavations made during the 1920's of the Neolithic flint mines at Blackpatch in Sussex, from a level probably, though not certainly, belonging to the period of mining.

In the Summer of 1982 the British Museum carried out a limited excavation of the similar flint mines at Harrow Hill (TQ 083100), about 1.5 km N.W. of Blackpatch. A sample of shelly colluvium from shaft 13c, immediately above the chalk backfill within a gallery, yielded a remarkably rich molluscan fauna of 31 species, including 18 examples of *Lauria cylindracea* (da Costa) and 5 examples of *L. sempronii*. *Corylus* charcoal from the same sample gave a radiocarbon date of  $4670 \pm 60$  B.P. (BM-2071). The fauna is purely of woodland character, and suggests strongly that the flint mines were being dug in forest.

I am indebted to Mr G. Sieveking and Mr R. Burleigh of the British Museum for allowing me to visit the excavations and for providing the radiocarbon date.

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# NEW DISTRIBUTIONAL DATA ON LAND MOLLUSCA FROM S. FRANCE

The following species of land Mollusca found in southern France in August and September 1980 apparently represent new distributional records.

*Acicula fusca* (Montagu) Three sites in the Dordogne (UTM squares: CK27, CK48, CK69; see also Preece & Willing, *Conch. Newsl. Lond.*, No. **59** (1976) p. 541).

*Columella* cf. *columella* (Martens) Grassy ledges of limestone crag at c. 1800 m elevation, 3 km below Port de Gavarnie, Hautes-Pyrénées (YN43). The single mature shell and three immatures show precisely the same shape and form of apex as Swiss and Norwegian *C. columella*. However, additional material needs to be studied before this arctic-alpine species can be confidently recorded from the Pyrenees.

*Vertigo angustior* Jeffreys Three records from the Dordogne: living in a small fen (CK16), and dead shells from stream debris (CK27, CK58).

*Planogyra sororcula* (Benoit) Beneath stones and at base of varied herbs and grasses on moist ledges of limestone crag at c. 1800 m elevation, 3 km below Port de Gavarnie, Hautes-Pyrénées (YN43). The only published record from the Pyrenees is from Prov. Huesca, Spain (Gittenberger, Menkhorst, & Raven, *Basteria*, **44** (1980) p. 11), although Raven (*Basteria*, **44** (1980) p. 54) also records it from the Cantabrian Mountains in Prov. León, Spain.

*Helicodiscusingleyanus* (Pilsbry) One fresh shell sieved from leaf-litter of deciduous woodland on limestone slopes at Grotte de Sare, c. 15 km SE. of St. Jean-de-Luz, Pyrénées-Atlantiques (XN19). The species was first recorded from France by C. O. van Regteren Altena (*Basteria*, **25** (1961) pp. 41–43) but it has not hitherto been reported from this region.

*Semilimax* cf. *pyrenaicus* (Férussac) Empty shells and living immature animals from two places in Dordogne (CK46, CK56). The shells resemble this species rather than *S. semilimax* (Férussac) (cf. Preece, & Willing, *Conch. Newsl. Lond.* No. **59** (1976) p. 541).

*Phenacolimax annularis* (Studer) Besides sites at high elevations in the Pyrenees, this species was found near the valley floor (c. 600 m elevation) in a limestone quarry S. of Sarrancolin, Hautes-Pyrénées (BH86), showing the range is less strictly high-montane than suggested by the literature.

*Aegopinella minor* (Stabile) Dry limestone scree partly shaded by hazel *Corylus avellana* L. scrub, 1 km S. along D116 road from Villefranche-de-Conflent, Pyrénées-Orientales (DH41). The specimen has a characteristically long, slender, curled distal portion of the penis (as shown by Forcart, *Arch. Molluskenk.* **88** (1959) p. 15, Abb. 1). This appears to be the first Pyrenean record, although the species is known from similar dry calcareous places in both the S. Alps and Catalonia, Spain (Riedel, & Vilella, *Misc. zool. Barcelona* **2** (1968) p. 11; Riedel, *Fragmenta Faunistica Warszawa* **15** (1970) p. 388).

*Milax rusticus* (Millet) Two slugs from mixed deciduous woodland on a limestone slope at La Roque St. Christophe, Dordogne (CK48) appear to be the first record from SW. France, although Dr. M. P. Kerney (pers. comm.) also found this species in the Dordogne in 1980.

*Limax nyctelius* Bourguignat One found creeping on a concrete interior wall of a camp-site toilet, Siorac-en-Périgord, Dordogne (CK46). Dissection showed a long 'S' shaped penis without flagellum. This is apparently the first record from France.

*Macrogastrea ventricosa* (Draparnaud) Living on shaded ledges of limestone rock near head of Gorge de la Fou, SW. of Perpignan, Pyrénées-Orientales (DH61). The shells differ from shells collected near Geneva in having markedly finer ribbing and a narrower mouth. There appears to be no other record from the Pyrenees, although Zilch & Jaekel *Die Tierwelt Mitteleuropas, Ergänzung* (1962) p. 156) list N. Spain.

*Trochoidea geyeri* (Soós) Shells from around dry unshaded limestone rocks at Arabaux, NE. of Foix, Ariège (CH86) appear to be of this species. They differ from shells of *Helicopsis striata* (Müller) in having a smaller protoconch (cf. Sparks, *J. Conch., Lond.*, **23** (1953) p. 372). There are apparently no other records from S. France.

*Trochoidea (Xerocrassa) penchinati* (Bourguignat 1868) (synonym *monistrolensis* Fagot 1884) Living beneath grass and herbs on limestone bank by D611 road, 50 m NW. of junction with D59 road, 7 km S. of Tuchan, Pyrénées-Orientales (DH74). The specimens were identified by Dr. E. Gittenberger who commented (*in litt.*) that this species has hitherto been reported only from E. and NE. Spain. It was identified primarily from the anatomy of one live-collected snail, but the shell characters also allow identification, with strong radial ribs, keeled periphery and hairs or hair-scars occurring all over the shell.

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## FRESHWATER MOLLUSCA ON BANKS ISLAND, ARCTIC CANADA

Non-marine Mollusca were studied around Sachs Harbour, SW. Banks Island, N.W.T., Canada (72°N., 125°W.) in July and August 1981. This region has a severe climate, with mean annual air temperatures of –14°C (February mean –31°C., July mean +5°C.). It is within the zone of continuous permafrost and has open tundra vegetation. No terrestrial Mollusca were found despite extensive searches and field-sieving in varied habitats, and none have been reported from this far north in arctic Canada.



*Aplexa hypnorum* (L.) was the only freshwater mollusc hitherto known on southern Banks Island (Clarke, *The Freshwater Molluscs of Canada*, Ntl. Musm. Canada (1981)). *A. hypnorum* was found at several places near Sachs Harbour in 1981. In addition, *Pisidium conventus* Clessin was recorded from Fish Lake, 30 km SE. of Sachs Harbour, providing the first record of a living freshwater bivalve from Banks Island. The species was hitherto known to occur north to southern Victoria Island (Clarke, *op. cit.*).

These provide the northernmost records of freshwater Mollusca from North America, so it is noteworthy that both species were living in environments that had thermal regimes very different to those implied by the air temperature measurements.

*A. hypnorum* was found only in small, shallow, unshaded pools; mostly these were less than 1 m across and none were more than 5 m across, with depth 0.1–0.5 m. The pools were normally floored and surrounded by a mat of mosses (*Scorpidium scorpioides* (Hedw.) Limpr., *S. turgescens* (T. Jens.) Loeske) and there was often emergent vegetation of *Carex aquatilis* Wahlenb. or *Arctophila fulva* (Trin.) N. J. Andersson. These small pools were mostly developed in lines resulting from thermal degradation of ice-wedges. Water temperatures were measured in pools with a mercury-bulb thermometer accurate to  $\pm 0.5^\circ\text{C}$ . On clear sunny days with light winds the water temperatures were normally considerably in excess of air temperatures. For example, on 23 July 1981 at 1400 hours the air temperature was  $9^\circ\text{C}$ ., rising to  $11\text{--}12^\circ\text{C}$ . near the soil amongst herbs. However, water temperatures in the small pools were  $15\text{--}18^\circ\text{C}$ ., the highest readings being obtained from amongst open moss and *Carex* growth near the water surface. On overcast days such solar heating of shallow pools did not occur. Although these pools may have the water heated to above air temperature on many days during the short arctic summer, the pools are completely frozen for eight to nine months of each year.

During warm sunny weather *A. hypnorum* was seen to spend much of the time feeding actively at and close to the water surface, behaviour that would allow the fullest benefit to be derived from solar heating of the water. The translucent shell and black mantle pigmentation may also be adaptations to improve absorption of radiant heat. It is noteworthy that the Banks Island specimens have shells with much shorter spires than those from lower latitudes (shell heights of adult animals 11–18 mm). This more stocky body form may reduce the rate of heat loss and hence prolong activity as temperatures fall.

In Britain *A. hypnorum* is well known as a colonist of temporary pools: it often breeds during the winter in pools that dry in summer (Boycott, *J. anim. Ecol.*, **5** (1936) pp. 116–186).

*Pisidium conventus* was found in the stomachs of two char *Salvelinus* caught from deep in Fish Lake. This large lake is more than 10 m in depth and no *Pisidium* could be found in the shallow edges of the lake. *P. conventus* was thus apparently living beneath the depth of winter freezing, where it would be effectively insulated by the winter ice but receive little heat in summer.

It may be estimated from information on the air temperatures combined with data on the insulating effects of snow and ice (cf. Washburn, *Geocryology*, Edward Arnold (1979)) that on Banks Island individual *A. hypnorum* experience an annual temperature range from below  $-20^\circ\text{C}$ . to  $+18^\circ\text{C}$ ., whereas *P. conventus* would experience a range of c.  $+1^\circ\text{C}$ . to  $+4^\circ\text{C}$ . Freshwater Mollusca were conspicuously absent from many hundreds of large ponds and small lakes that did not have either of these two kinds of favoured thermal environment.

Late Pleistocene interglacial deposits exposed in the cliffs at Duck Hawk Bluff near Sachs Harbour (J.-S. Vincent, in preparation) contain shells of two freshwater gastropods that are not known to live on Banks Island at the present day, *Valvata sincera helicoidea* Dall and *Stagnicola arctica* (Lea) (nomenclature follows Clarke, *op. cit.*), implying that temperatures in this interglacial were warmer than at present to allow these species to occur further north. However, the observations described above show that thermal regimes in some arctic freshwater microhabitats may differ widely from those implied by air temperatures, due to marked insulating effects of ice and snow, or to solar radiation heating shallow water. Hence detailed inference of palaeotemperatures from cold periods of the Pleistocene based on fossils of freshwater animals may be confused by differences between microhabitats.

Thanks are due to N.E.R.C. for funding and Polar Continental Shelf Project for logistic support.

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## ADDITIONAL FOSSIL AND ISOTOPIC EVIDENCE FOR THE AGE OF THE INTERGLACIAL TUFAS AT HITCHIN AND ICKLINGHAM

The interglacial tufas at Icklingham, W. Suffolk (Kerney, *J. Conch., Lond.*, **29**, (1976) pp. 47–50) and Hitchin, Hertfordshire (Kerney, *Proc. Geol. Ass.* **70**, (1959) pp. 322–337) have much richer assemblages of fossil land snails than other British Middle Pleistocene deposits. Amongst species recorded are some that no longer occur in Britain and for which there are few other British records (*Acicula polita* (Hartmann), *Semilimax* cf. *semilimax* (Férussac), *Laminifera pauli* (Mabille), *Ruthenica filograna* (Rossmässler) and *Macrogastera ventricosa* (Draparnaud)), two of these species apparently being completely extinct (*Acicula diluviana* (Hocker) and *Retinella* (*Lyrodiscus*) *skertchlyi* Kerney



1976). *R. (L.) skertchlyi* may be a synonym of *R. (L.) jourdani* (Michaud 1882) (Kerney, *Conch. Newsletter, Lond.*, No. 72, (1980) pp. 217–218); it has recently also been recorded from Pleistocene cave deposits in the Mendips (Ellis, *J. Conch., Lond.* (1983) **31**, p. 191). This note lists additional Mollusca obtained from recent investigations, and finds of small mammals that allow the age of the Hitchin tufa to be estimated more accurately.

Large samples of the Hitchin tufa have provided material of nearly all the molluscan species listed by Kerney (1959). In addition, single shells were found of *Valvata cristata* Müller and Succineidae sp. (a shell apex).

Samples from the Icklingham tufa provided several additions to the published list, the most notable being *Laminifera pauli* (3 apices, 1 mouth and several fragments). The genus *Laminifera* is now restricted to the western Pyrenees; it was hitherto known from the British Pleistocene only from the Hitchin tufa. Thus the occurrence of *Laminifera* at both Hitchin and Icklingham adds further weight to evidence given by Kerney (1976) that they are of similar age. The Icklingham shells were sufficiently well preserved to show that specific identification as *L. pauli* is justified; additional material from Hitchin is more fragmented but similar. *L. pauli* has also been recorded from a 'Holsteinian' tufa at St. Pierre-les-Elbeuf, France (Lautridou, *The Quaternary of Normandy*, in Quaternary Research Association, Field Handbook Normandy Meeting May 1982, p. 41).

Other additions to the list of Mollusca from Icklingham are *Valvata piscinalis* (Müller) (1), *Bithynia* cf. *tentaculata* (L.) (1), *Lymnaea truncatula* (Müller) (4), cf. *Segmentina nitida* (Müller) (1), Succineidae sp. (1), *Discus rudatus* (Férussac) (4), *Zonitoides nitidus* (Müller) (1), *Sphaerium lacustre* (Müller) (1 valve + fragments) and *Pisidium personatum* Malm (5 valves). A tooth from the Icklingham tufa was identified by Dr. A. J. Stuart as wood mouse, *Apodemus* cf. *sylvaticus*.

Teeth of various small mammals were obtained from the Hitchin tufa and these also were identified by Dr. Stuart. This material comprised: bank vole, *Clethrionomys glareolus* (Schreber) (one M<sup>2</sup>, one M<sub>2</sub>, one incomplete molar); extinct water vole, *Arvicola cantiana* (Hinton) (one M<sub>2</sub>, one fragmentary M<sub>3</sub>, one molar fragment); *Arvicola* sp. (two incisor fragments); wood mouse, *Apodemus* sp. (one I<sup>1</sup>). Earlier records (Kerney 1959) included the extinct pine vole, *Pitymys* cf. *arvaloides* Hinton (det. J. N. Carreck).

The record of *Arvicola cantiana* is significant for interpretation of the age of the tufa. This vole is thought to have evolved from *Mimomys savini* Hinton, the form represented in the Cromerian at West Runton, and to have given rise to the modern water vole, *Arvicola terrestris* L. during the Devensian (Koenigswald, *Eiszeitalter Gegenwart*, **23–24**, (1973) pp. 159–167, Stuart, *Pleistocene Vertebrates in the British Isles*, Longman, 1982). However, occurrence of *Pitymys* implies a Hoxnian or older age (cf. Sutcliffe & Kowalski *Bull. Brit. Mus. (Nat. Hist.)*, Zool., **27** (1976) pp. 31–147, Stuart, *op. cit.*), a conclusion supported by the molluscan evidence (Kerney, 1959).

The earliest records of *A. cantiana* come from interglacial deposits at Ostend, Norfolk (Stuart & West, *Geol. Mag.* **113** (1976) pp. 469–473) and Westbury-sub-Mendip, Somerset (Bishop, *Spec. Papers in Palaeontology* No. 28, 1982) assigned either to the late Cromerian or to an interglacial between the Hoxnian and Cromerian. The Hitchin tufa might therefore be late Cromerian, Hoxnian or from this 'Westbury interglacial'. Presence of numerous erratic pebbles including far-travelled types in the gravels beneath the Hitchin tufa (Kerney 1959) suggests a post-Anglian age (i.e. Hoxnian in view of the mammalian evidence), although an earlier glaciation of south-central England has since been inferred (e.g. Shotton *et al.*, *Phil. Trans. R. Soc.*, B **289**, (1980), pp. 55–97).

Attempts were made to obtain uranium-series disequilibrium dates on samples of the tufa matrix from both sites. Samples from Icklingham yielded <sup>230</sup>Th/<sup>234</sup>U activity ratios within <1 s.d. of unity. Thus the samples are probably >300 k yr B.P. in age. Minimum age estimates on two parts of the same sample using a 1 s.d. criterion were >220 k yr (HUTH- 1362) and >285 k yr (HUTH- 1540). A sample from Hitchin (HUTH-1361) showed evidence of post-depositional leaching of uranium, giving a <sup>230</sup>Th/<sup>234</sup>U activity ratio of much greater than unity which therefore could not be converted to an age estimate.

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## A LETTER FROM WILLIAM TURTON

In his recent article on marine molluscs described by W. Turton and W. Clark (*J. Conch., Lond.* **31** (1983), pp. 161–71) Anders Warén says that not very much is known about the life of William Turton. Apart from his writings, indeed, virtually nothing substantial is known about Turton, though he has always been presented as a rather endearing fellow.

Less celebrated as a scientific personality than as a well-meaning but gullible pioneer of British conchology, he deserves to be known as more than the shadowy author of several light-weight books and articles about shells. Consequently it is worth reproducing here the words of a holograph letter he wrote in 1828—seven years before his death and three years before the publication of his well-known *Manual of the Land and Fresh-water Shells of the British Islands*.



The recipient of the letter is not named but internal evidence indicates that it was either Joshua Alder of Newcastle or William Bean of Scarborough, illustrious conchologists both. Each of them assisted Turton by giving him specimens and information which he requested while preparing his *Manual*. The letter, long in my possession, occupies two sides of a single sheet of paper. The handwriting slopes strongly to the right and shows tell-tale signs of infirmity in the writer. Evidently William Turton was well past his prime when working on his *Manual*. This knowledge only endears him to us more.

Bideford, Devon  
April 12, 1828

Dear Sir

Your very acceptable packet came safe to me yesterday. Many thanks for its contents. Of the *Vertigo palustris* I had not before a quite perfect specimen, and the *Turbo tridens* are finer than any in my Cabinet. The two *Clausilia* are without doubt the *Cl. parvula*. The lip of one is broken, and when you can spare a couple more I shall be glad of them.

Of the shells found by Mr. Hutton I can at present form no clear guess. They may be either of the *Bulimus* tribe or the *Cyclostoma*. The former genus has the mouth oval, without a lid. the latter genus has the mouth round, and furnished with a lid. The fresh water shells of Draparnaud are now properly removed into a separate genus, named *Paludina*.

A long fit of illness and a long absence from home has made me very negligent in my various correspondence, and as the sailors say I must try and bring up my lee way.

Mr. Gibson's Chitons I will forward as soon as I have leisure, with what I can spare for Mr. Hutton. If he gets more of his mountain shells I will thank him to save me a specimen. I shall in the next package I send forward some shelly sand just come from the Land's End in Cornwall in which will be found some interesting things. I will also send two specimens each of the *Bulimus lineatus*, and *Bulimus clavulus*, one of each for yourself and the others for Mr. Hutton, all I can possibly spare, as they are of very great rarity, and I despair of being able to get more.

I am, My dear Sir  
Yours most truly  
*W. Turton.*

S. PETER DANCE,  
South Bank House, Broad St, Hay-on-Wye, Powys HR3 5DB











## INSTRUCTIONS TO AUTHORS

Manuscripts should be sent to:— **Dr M. P. Kerney, Department of Geology, Imperial College, London SW7 2BP.**

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**COMMUNICATIONS** These are intended to be short notes of an original nature which do not merit the treatment of a full paper. *Communications* must not contain any figures, tables or plates and should conform in style to that of recent issues of the *Journal*.



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# NON-MARINE CONCHOLOGY OF CORNWALL AND THE ISLES OF SCILLY

STELLA M. TURK\*

(Presidential Address, delivered before the Society 19 March, 1983)

*Abstract:* Due to its geology and topography together with disruptive activities associated with mining and deforestation, Cornwall has a paucity of non-marine Mollusca. Nevertheless the land that has been 'pitted' during the extraction of alluvial tin, ensures continuance of wetland, supporting such nationally local species as *Lymnaea glabra*. On the cliffs, the Lusitanian snail *Ponentina subvirescens* is locally common. Cornish stone 'hedges' serve as an important habitat and as refuges, whilst gardens support a wide range of synanthropic species as well as 'woodland' types. Dunes of blown shell sand have a rich calcicole and xerophile snail fauna, including *Theba pisana* and *Pomatias elegans*, and enshrine valuable subfossil material relating to the change from 'woodland' to 'open country' species. The fauna of the main habitats is discussed, and an annotated check list is appended. A short summary of non-marine molluscan studies in the county reveals the strong influence of the Conchological Society.

## INTRODUCTION

In contrast to its wealth of marine Mollusca (Turk 1983), Cornwall and the Scillies are decidedly poor in their non-marine molluscs. Of nearly 200 species recorded in Britain (Kerney 1976), the Cornish mainland has 117 of which 55 occur in the Isles of Scilly, but only 50 to 60 species are common in Cornwall in the sense of being present in large numbers in many ten kilometre squares. These numbers compare with 135 for Devon and over 160 for Oxfordshire, one of the richest counties for non-marine molluscs. However, the humidity and mildness favour slugs, with 19 of the 24 British species represented, many of them being exceedingly plentiful. Apart from the stunted nature of many of its molluscs, there is no record of any varieties peculiar to the Cornish mainland. On the Isles of Scilly Richards & Robson (1926) did find that 12 species showed differences of 'slight order' from those of the Land's End but these did not exceed in magnitude the differences usually found between colonies in the same area but not immediately adjacent to one another. The reasons for dwarfing and paucity of numbers may be categorised as follows:

- 1 There is a virtual absence of calcareous substrata apart from a very small outcrop of limestone in south-east Cornwall, and the dunes of blown sand which are mainly on the north coast. Boycott (1934, p. 9) writes 'Increasing experience has led me to attach more and more importance to lime.'
- 2 There is a scarcity of deciduous woodland, especially in the western half of Cornwall which has never recovered from earlier deforestation. As early as Domesday (1085 A.D.), the south-east of the county was the only markedly wooded part, and by 1615 so much wood had been used for tin-smelting, that it was being imported from Devon. In such a wind-swept county, once trees are felled it is very difficult to re-establish them.
- 3 Much of the land surface is contaminated with inimical substances like arsenic, copper, lead and zinc, and it may remain bare for decades, or only have a light covering of poor-soil grasses, mainly *Agrostis* spp., succeeded by ling (*Calluna vulgaris*). In 1965, there were 33,014 acres of spoil tips in England, 41% of which were in Cornwall, with less than 2,000 acres considered worth reclaiming (*Western Morning News* for 7.12.1966)

\*Shang-ri la, Reskadinnick, Camborne, Cornwall, TR14 0BH.





Fig. 1. Landscape and habitats of Cornwall adapted by Mrs Patricia Burton from the Cornwall County Council Landscape Map by permission of C. G. Griffin M.A., County Planning Officer (Based upon Ordnance Survey Map with permission and acknowledgement to HMSO).



4 The rapid and relatively short streams, mainly cutting across the county, are not conducive to the existence or dispersal of most freshwater molluscs. Many of the streams have been polluted with mine 'tailings' in the past, and this still happens in the Red River which empties into St Ives Bay. Until 1970, streams in the St Austell district were white with waste from china clay processing, and indeed several still run white after prolonged rainfall. However, as a result of mining and quarrying associated with tin, copper, china clay, serpentine and granite, pools are plentiful. Tin mine pits may mature to support a reasonably diverse fauna and flora, but many contain so much iron that iron-fixing bacteria produce an unfavourable environment. Most of the china clay pits are deep and steep-sided and remain oligotrophic.

## GEOLOGY

Most of the county is covered by a Devonian slaty rock known to Cornish miners as 'killas', but in the north-east this is replaced by non-coal-bearing Carboniferous rocks. A disjunct granite spine stands above the surrounding landscape in Devon (Dartmoor) and Cornwall (Bodmin Moor; the Hensbarrow area including St Austell district; Carnmenellis covering Camborne and Redruth); Land's End; and lastly the Isles of Scilly. These granite 'bosses' are ringed by the metamorphic aureoles producing such minerals as copper, tin and lead which have made Cornwall famous and which have drastically changed the landscape as a result of mining over the centuries. Few species of Mollusca live on granite (Ellis 1926, p. 44) and even fewer survive when the area has been disturbed by mining. In the Lizard peninsula, serpentine, gneisses and schists form a complex entity of which the serpentine is famous for supporting many plants otherwise found only on calcareous soil (Coombe & Frost 1956) but which does not favour calcicole molluscs. By contrast they are favoured on the north Cornish coast, where extensive dunes have been formed, reaching 82 m above sea level on the Perranporth cliffs and a depth of 60 m at Hayle (Barton 1964, p. 164).

## CORNISH HABITATS AND SPECIES

### *Flowing or lentic waters*

The molluscan fauna of Cornish streams is very predictable and very meagre, especially in the Land's End peninsula, as lamented by Wright & Adams (1905, p. 223) who write 'The numerous streams rushing from high inland sources over rocky beds without weed or moss seem absolutely destitute of bivalves.' In fact the only bivalves in Cornish streams are *Pisidium* spp. and the only one likely to be present in fast-running water is the ubiquitous *P. casertanum*. Of the gastropods, *Ancylus fluviatilis* is abundant in fast stony streams, and even extends its range down to shore level (Verdcourt 1945 and personal observation). All streams, with hard or soft substrata, unless heavily polluted with iron waste from mining activities, contain populations of *Potamopyrgus jenkinsi* which Kerney (1966, p. 9) states sometimes competes with our native fauna to a disastrous degree. It is now believed to be an introduction, probably from New Zealand, and was confined to brackish water in this country until it started to invade freshwater towards the end of last century (Fretter & Graham 1978, p. 132). The same authors give its first record in the South-West as 1893 when it was found in the River Exe. In Cornwall it was not recorded until 1919 (at Looe, by C. E. Burton) and by the early 1940s it was so abundant at some sites as to darken the substratum, particularly when the shells themselves were blackened with heavy manganese deposits as in the stream at Trelassick near Truro (personal observations). Forms with a keel of periostracal



hairs are rare, but in the stream at Porth Hellick, St Mary's, Isles of Scilly, where specimens were first collected by Canon J. H. Adams in 1953, they seem to be the only form (personal observation).

Most Cornish rivers are too shallow, the water too soft and, in their lower reaches, too saline, to favour the larger bivalves and gastropods, so their fauna is more reminiscent of streams than rivers. An exception is the River Tamar which forms the boundary between Devon and Cornwall. This, the largest 'Cornish' river, contains the soft-water pearl mussel, *Margaritifera margaritifera*, otherwise unknown from Cornwall apart from the River Camel (Couch 1841, p. 32). *Anodonta anatina* occurs in Tamar Lake, a catchment area of the Tamar and now a reservoir, and the Bude Canal. These are the only two authenticated sites for *Pisidium amnicum* and the very local *P. moitessierianum*. *Lymnaea peregra* is plentiful where there is weed.

#### *Still or lotic waters, including all wetland sites*

Cornwall has an abundance of small ponds and pools, many of them a legacy of past tin extraction. For instance, on Porkellis Moor near Helston there are 21 'major pools' in 105 hectares (Johnson & Holliday 1978) and a larger number on Red Moor near Lostwithiel: the former has low level alluvial gravels, and the latter high level deposits, both being rich in tin. Larger pools have resulted from china clay extraction, stone-quarrying and the formation of boating and ornamental lakes, but until the proliferation of reservoirs in the past few decades, there were few large expanses of water in the county, which has only three sizable natural bodies of water: Loe Pool near Helston and Swanpool near Falmouth (the latter brackish since 1826), both formed by marine shingle bars, and Dozmary Pool on Bodmin Moor.

*Potamopyrgus jenkinsi* and *Lymnaea peregra* are the only constant species present in such habitats, the latter being represented by the large var. *ovata* Draparnaud in ornamental pools on the Scillies as well as the mainland. *Lymnaea stagnalis* has become established in a few estate and quarry pools as at St Columb Major (the only record mapped by Kerney (1976)) but the shells are invariably thin with eroded spires.

By contrast, on the dunes at Phillack near Hayle, a pool about a metre deep surrounded by calcium-rich sand, contains a large colony of *Sphaerium lacustre*, a local species in western Britain. Associated species *Potamopyrgus jenkinsi*, *Anisus leucostoma*, *Lymnaea stagnalis* (large and thick-shelled) and small numbers of *L. glabra*. This is an unusual site for *L. glabra* which usually lives 'in mean places where few if any other molluscs care to live—shallow grassy ditches and ponds which usually dry up in the summer, sometimes in marshes' (Boycott 1936, p. 128). With the drainage of marshes, this species may soon be considered endangered. One of its classic sites was at Sennen where it was first found by Templer (1857) but these small pools have recently been filled in. However, in Cornwall, the amount of mineralised marshy land ensures plenty of sites, potential and actual, as it has been found in eight post-1950 localities, each in a different 10 km<sup>2</sup>. Apart from the pool at Phillack, described above, most dune slacks in Cornwall are shallow and dry out in hot weather; nevertheless in areas where dwarf willow grows, there is often an abundance of *Potamopyrgus jenkinsi*, *Lymnaea peregra*, *L. truncatula* and *Anisus leucostoma* together with *Deroceras laeve* and other slugs which would find the surrounding dunes too dry.

*Physa fontinalis* is a hard-water species which is rare in western Britain, and the only Cornish records are one at Falmouth in the 1840s and another from an artificial pond at Glendurgan where it was found in 1974 by Mr D. C. Long who considered that it might have been introduced with plants. *P. cf. heterostrophia* is common at Swanpool, Falmouth, whilst *P. cf. acuta* appeared in a newly-dug garden pool at Reskadinnick, Camborne a few years ago.



Apart from *Anisus leucostoma*, the only other common planorbid is *Gyraulus albus* which lives in cleaner deeper water. There are several 19th century reports of *Armiger crista*, but only one 20th century site is known, at Kennack, Lizard peninsula.

The fact that many Cornish wetland sites are on mining wasteland (including sites on the Lizard heaths where serpentine has been extracted) that is not easily reclaimable for any purpose, means that succession from pools to marshes progresses unchecked by artificial drainage, providing additional sites for those species that can resist drying out, such as *Lymnaea truncatula*, *L. palustris*, *L. glabra*, *Anisus leucostoma* and the bivalves *Pisidium obtusale* and *P. personatum*, this last being described as a molluscan slum dweller by Ellis (1978, p. 62). *Pisidium milium*, *P. nitidum* and *P. subtruncatum* are typical of the deeper water of ornamental and boating lakes. In 1971, J. E. Lewellyn Jones (pers.comm.) found the last two in Dozmary Pool, high on the peaty land of Bodmin Moor, so very sparse in molluscan life.

In marshy conditions, *Zonitoides nitidus* is common, often in association with *Deroceras laeve* which is probably under-recorded for Cornwall. Occasionally found are *Acicula fusca*, *Columella edentula*, *Vertigo antivertigo* and *V. substriata*. *Succinea putris* occurs on waterside vegetation, but is distinctly less common than *Oxyloma pfeifferi* which is sometimes found submerged.

It is rare to find more than five or six aquatic species in any one site (J. Humphreys pers.comm. and my own observations) and a further indication of the paucity of Cornwall's freshwater molluscan fauna is given by Kerney & Stubbs (1980, p. 20): of 12 species which they list as indicative of good freshwater habitats, only one occurs in Cornwall, in the Bude Canal.

## Dunes

The sandy bays from Land's End to Bude are backed by high and extensive dunes. The sand itself results from the comminution of rock and marine shells, the latter often forming at least 60% of the sand, making it readily air-borne and very high in lime content: at Harlyn Bay it can produce as much as 9.5 cwt of lime per ton of sand (Hawk 1929). The snails that live on the dune vegetation are so numerous that the surface soil remains very alkaline even as much as 1 km from the sea, unlike the majority of dunes which quickly become less alkaline as the humus increases (Hepburn 1944, p. 183). On the south coast of the county, the dunes are very small and not found east of Par. The Isles of Scilly have a well-developed dune system on Tresco, and smaller dunes on the other main islands, but the Scillonian dunes are less alkaline than those of the mainland due to the higher proportion of granite fragments which impart a characteristic whiteness to the sand.

Evans (1972, p. 175) draws attention to the fact that *Helix aspersa* is a common sand dune species in Cornwall, living in association with *Cochlicella acuta* and *Cernuella virgata*, but despite the fact of it frequenting wild coastal habitats in the far South-West, there is no evidence that it existed here prior to the Roman era from which the first British records date. The shells of *Helix aspersa* in these calcareous conditions are very thick and heavy. The above three species, together with *Candidula intersecta* and *Cepaea nemoralis* are all abundant on the dunes, but *Helicella itala* is distinctly less common, and being a calcicole it is rare on the Isles of Scilly: the single record dates from pre-1876 and it is one of the species which Richards & Robson (1926) failed to re-find on St Mary's. *Cepaea nemoralis* is generally plentiful but it is not uncommon to find large numbers of intact shells, some empty and some with the dead remains of the animals: Richardson (1979) argues that a large proportion of these have suffered heat death and that this is selective of particular colour/banding combinations. White and partially white varieties of *Helix aspersa* also occur on the dunes, and although no statistical work has been done on these, one might suppose that the same selection factors



would operate. *Cepaea hortensis* is almost never found on Cornish dunes, although it does live on duneland, especially in Scotland. It is not as common anywhere in Cornwall as *C. nemoralis*, and is distinctly scarce in the west of the county. Of especial interest and evidently present since the inception of the blown sand (Bullen 1902a and Whimster 1977), is the obligatory calcicole *Pomatias elegans* which is restricted to scrub growth, such as Wild Privet, on the dunes, although it is absent from many areas that seem suitable. Kerney (1968, p. 280 ff.) describes how it has declined since the Post-glacial Climatic Optimum, leaving relict populations.

The frost-tender, xerophilous and calciphilous snail, *Theba pisana*, has been used as an example of an ancient Lusitanian element, but its complete absence from any archaeological site in Britain suggests that it has been introduced within historic times, (Cowie (1982) suggests only about three centuries ago), possibly brought in accidentally with shipping, commerce or as food, since on the Continent (where it grows larger) it was commonly eaten (Lovell 1867, p. 16), and where Dr B. Coles (pers.comm.) saw it collected for food in 1981, at Perpignan in France. Its first localised British site was published at the end of the 18th century (Maton 1797, p. 227). This was at St Ives in Cornwall, and Turk (1966) and Humphreys (1976) give accounts of the history and ecology of the colony. In 1981 a much larger and more thriving colony was found at Treyarnon Bay (Humphreys *et al.* 1982) from where it is now spreading along the coast towards Constantine (Mrs J. A. Paton pers.comm.). However, Dr R. H. Cowie (*in litt.* 29.6.1983) writes that the colony is almost certainly not derived from the St Ives population which does not share the same shell morphs. The presence of a distinctly Mediterranean feature in the band formula '003' suggests to him a recent separate introduction from abroad. Cain (*in press*) describes and explains the genetics of the form '003' as well as the genetics of St Ives morphs.

Of the smaller species found on dunes, *Ashfordia granulata* is common at the base of sand-hill vegetation in Cornwall and the Isles of Scilly, as it is evidently more of a xerophile on the west coast of Britain than on the south and east (Evans 1972, p. 178), although allowance must be made for the greater humidity of western coastal sites. *Pupilla muscorum* is confined, in Cornwall, to dunes, but *Vallonia excentrica* occurs in other dry habitats: probably all Cornish subfossil records of *V. pulchella* refer to *V. excentrica* e.g. the hundreds of empty shells in dunes at Phillack near Hayle at depths 0.30 m to 9 m (Edmonds 1865). Lastly, *Vertigo pygmaea* is probably very common although frequently over-looked because of its small size.

The small sheep that grazed the dunes in the 18th century were said to provide 'the sweetest mutton' as the snails 'that spread themselves over the plains early in the morning . . . yield a most fattening nourishment to the sheep' (Borlase 1758, p. 286). The sheep must also have eaten many of the liver-fluke snails, *Lymnaea truncatula*, that are usually abundant in the slacks!

### *Cliffland, heathland and grassland*

Cornish cliffs away from the blown-sand areas, typically have a shallow acid soil with a heathland flora, giving way to maritime plants near to the cliff edges. The most obvious molluscs are the ubiquitous *Arion ater* agg., *Helix aspersa* and *Cepaea nemoralis*.

The most interesting cliffland species in terms of geographical distribution, is *Ponentina subvirescens* which in Britain is to be found only in Cornwall, Devon and Pembrokeshire, almost invariably by the sea, although it does occur on high moorland above Zennor, and a solitary example was found on Davidstowe Moor, five miles from the sea, in 1966 (J. Humphreys pers.comm. and pers. observation). Gardiner (1919) found it chiefly under the roots and stems around which Biting Stonecrop (*Sedum acre*) and Sheep's Sorrel (*Rumex*



*acetosella*) were growing, and he concluded that the latter was its favourite food; Ellis (1926) recorded it as being frequent under stones in some spots, especially at the base of English Stonecrop (*Sedum anglicum*); Oldham (1933) found it much more abundant in the large mats of Sea Campion (*Silene maritima*), associated with other species which find food and shelter in such clumps: these included *Cochlicopa lubrica*, *Lauria cylindracea*, *Discus rotundatus*, *Clausilia bidentata* and *Vitrina pellucida*, all 'woodland' species. Boycott (1934, p. 24) especially notes the occurrence of *Clausilia bidentata* on sea cliffs in Cornwall, and J. Humphreys (pers.comm.) notes that these are invariably much smaller than those from inland habitats. On heathy hillsides near the sea in the Land's End district Ellis (1926) found all the above species, except *Vitrina pellucida*, under stones and at the bases of plants: in addition, he recorded *Aegopinella nitidula*, *Oxychilus draparnaudi*, *O. cellarius* and *Ashfordia granulata*. It will be noted that the whole assemblage of cliff heathland has much in common with the subfossil fauna beneath the blown sand, discussed later.

One of the few species to be found in acid grassland, is *Nesovitrea hammonis* which also lives in a variety of other habitats. *Columella aspera* is sometimes found in damp fields amongst rushes, tolerating more acid conditions than *C. edentula* (Paul 1975); although both species have been found in Cornwall, the former was only described in 1966 so that their distribution is still imperfectly known. The tiny subterranean snail, *Cecilioides acicula*, is mostly found on calcareous soils, and has a markedly coastal distribution in western Britain (Kerney 1976, map 135). In Cornwall it has as yet been recorded only at Looe, Tintagel and St Erth.

### Moors

Areas of high moorland, like Bodmin Moor with its peaty soils, are very unfavourable sites for molluscs. *Arion ater* agg., mostly the jet black form, is the only common species in the 'unimproved' areas. It must be noted however, that a vast part of Bodmin Moor, like other Cornish moorlands, has changed from heather moor to grass moor in the last century or so. The effects of this on molluscs has not been monitored.

### Woodland

Boycott (1934, p. 34) states that half the species of British molluscs 'live in ill-defined "woodland" habitats whose suitability varies in proportion to the shelter and lime they provide.' The molluscan fauna of a wood also depends on drainage, humidity, age and geographical location. Undisturbed woodland occurs in the Valency Valley near Boscastle and the Luxulyan Woods near Lostwithiel. The species lists closely resemble those of Torc Wood in Kerry, Ireland, an example cited by Boycott (1926, p. 26) as a particularly rich wood on acid soil with 24 species, although falling short of the 37 species listed for Whitcomb Wood in Gloucester, Boycott's example of a rich wood on calcareous (Oolite) substratum. The commonest species in such Cornish woods are *Carychium tridentatum*, *Cochlicopa lubrica*, *Lauria cylindracea*, *Discus rotundatus*, *Arion ater* agg., *A. intermedius*, *Vitrina pellucida*, *Vitrea crystallina*, *Aegopinella nitidula*, *Oxychilus cellarius*, *O. alliarius*, *O. helveticus*, *Zonitoides excavatus*, *Limax marginatus*, *Euconulus fulvus*, *Clausilia bidentata*, *Trichia hispida* and *Cepaea nemoralis*; less common are *Carychium minimum*, *Acanthinula aculeata*, *Punctum pygmaeum*, *Nesovitrea hammonis*, *Aegopinella pura*, *Balea perversa*, *Zenobiella subrufescens* and (almost confined to the east of the county) *Arianta arbustorum*; very rarely, *Ena obscura* and *Phenacolimax major* have been recorded. J. Humphreys comments (pers.comm.) that even beech woods are poor compared with beech woods in most other parts of southern England, perhaps in part due to the low lime



content of the soil and probably indicative of much disturbance in the past. *Limax cinereoniger*, an indicator of ancient woodland, occurs in the Valency and Luxulyan woods and in an old mining valley near Grampound, but it is a very scarce species.

### *Cornish hedges and dry stone walls*

The Cornish hedge is unique to the county, although its dry-stone walls are shared with other regions, including northern England and Wales. The main type of Cornish hedge is best described as a sandwich of earth between two stone walls, capped with turf. The combination of earth and stone of these remarkable edifices which span 2 m at the base and which are typically 2 m high, makes them a very important habitat, especially when, over the years, they become colonised with a diversity of plant cover, often including large trees and shrubs, themselves covered with lichens and mosses. Their importance is emphasised by Humphreys (1980) in writing of the snails of the St Ives district where the hedges of farms and moorlands provide valuable refuges for several species. Those typical of the county's hedges that are listed by him, are *Lauria cylindracea*, *Discus rotundatus*, *Clausilia bidentata*, *Trichia striolata*, *Cepaea nemoralis* and *Helix aspersa*, but additionally he found *Cochlicopa lubrica*, *C. lubricella*, *Vitrina pellucida*, *Aegopinella nitidula*, *Oxychilus draparnaudi*, *O. cellarius*, *O. alliarius*, *O. helveticus*, *Candidula intersecta*, *Cernuella virgata*, *Cochlicella acuta*, *Ashfordia granulata*, *Trichia hispida* and *Cepaea hortensis*. He did not record the slugs, many species of which are harboured in the lower and moister parts of Cornish hedges and considering that he was dealing with a part of Cornwall especially exposed to strong salt-laden winds, one can accept that Cornish hedges act as a significant reservoir for a wide range of species. Dry stone walls are not as rich, but like our hedges they provide perfect hibernacula as well as protection from extreme heat and predators. *Vallonia costata* likes dry situations and has been found on walls and banks, whilst *Pyramidula rupestris* is a typical wall species, but prefers limestone and consequently there are only a few scattered Cornish records. Some of the stone hedges represent an ancient and undisturbed habitat as they were erected as boundaries to Iron Age fields. Dating Cornish hedges by the numbers of trees and shrub species is probably not practical, since the hedges were not purposely planted in the first instance.

### *Gardens*

Gardens are so variable in size and the types of habitat that they encompass, that they defy precise definition. In such a notably stony county a rockery is often a feature, and the whole or at least part of the property may have a Cornish hedge as a boundary: add to these a pond, lawn, shrubs with an understorey of herbs and ground cover, plus a vegetable plot and it adds up to a considerable diversity of habitats each with its own 'community' of molluscs. Our own small cottage garden has all these features, and to date we have a total of 28 species. Twelve of these are slugs, including a southern form of *Arion ater* (non *rufus* fide S. M. Davies *in litt.* 1982), *A. lusitanicus* agg. *Deroceras caruanae*, *D. reticulatum*, *Boettgerilla pallens* (which seems to be replacing *Milax sowerbyi* and *M. budapestensis*), *Arion hortensis* agg. and *A. circumscriptus* agg., whilst *A. subfuscus* and *A. intermedius* are in the adjacent field but not in the garden. The commonest snails are *Discus rotundatus*, *Oxychilus cellarius*, *O. alliarius*, *O. helveticus*, *Trichia striolata*, *Cepaea nemoralis*, *Helix aspersa*, with *Clausilia bidentata* and *Lauria cylindracea* not uncommon on stones and on the cottage walls. The only species to have been deliberately introduced is *Planorbarius corneus* which maintains itself in very small numbers with an



abundance of naturally occurring *Lymnaea peregra*. In the larger gardens and estates, one expects more aquatic as well as 'woodland' species.

It is likely that markedly synanthropic types such as *Milax* spp. (except perhaps *M. gagates* which is often coastal in Cornwall), *Limax flavus* agg. and *Testacella* spp. are recent introductions. Just how rapidly species can spread when they are closely associated with humans, is shown by the S. E. European slug *Boettgerilla pallens* which has made a spectacular conquest of N. W. Europe and is now reckoned to be the commonest slug in Germany (Colville *et al.* 1974, p. 204). The same authors (op. cit.) record the first British occurrence of *Boettgerilla* in 1972 at Windermere, but it has now been found in several widely separated localities including, since 1975, Cornwall. *Testacella* spp., the worm-eating slugs, are rarely found far from cultivated places in this country. *T. maugei* was first reported from Bristol and in 1812 it was detected in Durdham Down Nurseries at Clifton (Taylor 1907, p. 21) from where it would soon have been widely dispersed with garden plants. This species is relatively common in Cornish gardens where it was first found in 1878 by Miss S. Hockin (Taylor 1907, p. 25). *T. haliotideia* was recorded in the 1880s by Marquand (1883, p. 406), but has not been found since whilst *T. scutulum* was found for the first time in some numbers in 1981 at St Ives in gardens and adjacent roadside verges (J. Humphreys pers.comm.) Many species e.g. *Limax maximus*, *L. flavus* seg. (which is sometimes a pest in Cornish back-kitchens) *Oxychilus draparnaudi*, *Trichia striolata* and *Helix aspersa* are to be found in a variety of habitats in Cornwall, although in the more northern parts of Britain they may be exclusively synanthropic.

#### SUB-FOSSIL EVIDENCE FOR THE ORIGINS OF THE CORNISH NON-MARINE MOLLUSCAN FAUNA

Kerney (1966) suggests that most of the rich molluscan fauna which existed in the British Isles during the Last Interglacial would have been wiped out by the extreme cold of the Last Glaciation, although a few hardy species such as *Lymnaea truncatula* and *L. peregra* might have survived in what are known to have been severe periglacial conditions obtaining as far to the south-west as Cornwall (Brown 1977). By 'about 5,000 B.C.' when the last link between the Continent and S.E. England was broken, our native fauna of land and freshwater Mollusca would probably have been complete, since the milder climate of c. 15,000 to 8,000 B.C. would have allowed a massive migration northwards (Kerney 1966, p. 5). Recent appraisal of the Late-Glacial and Post-Glacial scene as summarised by Dennis (1977) suggests that the Last Glacial involved a drop of 92 m in sea level, leaving the whole of the English Channel as dry land extending westwards to embrace the Isles of Scilly: he presents evidence for this land-link with the Scillies existing until between 7,000 and 8,000 B.C., although Professor Charles Thomas (pers.comm.) follows Hawkins (1971) in putting the land connection break in the 10th millenium B.C.

Various authors have recognized the importance of the conchological history enshrined in dunes of the far South-West where it has been surmised that many 'open country' species could be early colonisers from the south. Using the example of the Hebridean dunes, Evans (1972) deduces that none of the west coast dunes (machairs in Scotland, towans in Cornwall) are older than c. 3,000 B.C. A summary of the evidence for Cornwall is given in Caseldine (1980).

The stratigraphical and archaeological evidence presented for the pre-Iron Age status of certain species is considered inadequate by Kerney (1966, p. 10), although he recognizes that such coastal habitats in Cornwall would have provided ideal refuges for xerophiles during the forest phase of the Post-glacial. He instances the unreliable chronology in the work of Bullen



(1901, 1902a, b, 1912), Kennard & Warren (1903) and Woodward (1908): dunes are peculiarly liable to disturbance by burrowing mammals, and moreover Bullen was excavating a graveyard! However, re-examination by Whimster (1977) of the Harlyn sites described by Bullen, together with a scrutiny by Whimster of the more detailed excavation notes made by Bullen and held in Cornwall County Museum, confirms that the cemetery is correctly dated as Iron Age. Whimster himself (1977, p. 72) found a number of shells in an undisturbed soil layer below a building, itself at a lower level than the Iron Age graves: a charcoal sample from soil adjacent to this building was dated at c.2,000 B.C. by  $^{14}\text{C}$  analysis, giving this as an approximate start of the present Cornish dune system, assuming it would have been the same elsewhere on the Cornish coast. The species recovered from the pre-Iron Age layer were *Pomatias elegans*, an obligatory calcicole, *Cochlicopa lubrica*, *Ashfordia granulata*, *Cepaea nemoralis* and *C. hortensis*; in comparable layers, Bullen (1902a) found the same species with the exception of *Cepaea hortensis*, and the addition of *Vallonia excentrica* (recorded as *V. pulchella* but re-determined by Dr M. P. Kerney from the original material which is in the County Museum) and two species for which pre-Iron Age evidence in Britain has not yet been accepted, *Cochlicella acuta* and *Ponentina subvirescens* (recorded as *Hygromia montivaga* West.). Davis (1956) also recorded *P. subvirescens* in a pre-Iron Age site at Trebetherick the earliest layer of which he dated as Mesolithic or earlier.

These findings accord well with those of Kennard & Warren (1903) who list *Cochlicopa lubrica*, *Vallonia pulchella* agg., *Discus rotundatus*, *Arion ater* agg. *Aegopinella nitidula*, *Oxychilus cellarius*, *Clausilia bidentata*, *Cepaea nemoralis* and *C. hortensis* from what they consider to be probably Neolithic levels at Towan Head, Newquay, and they show how these species, most of which need a modicum of shade, are replaced by the drift-soil snails *Pupilla muscorum*, *Cernuella virgata*, *Helicella itala* and *Cochlicella acuta*. A further and more detailed examination of the Towan Head site by Woodward (1908) revealed in addition to the records of Kennard & Warren, *Pomatias elegans*, *Carychium minimum* agg., *Vertigo pygmaea*, *Acanthinula aculeata*, *Nesovitrea hammonis* and *Oxychilus draparnaudi*: this last species was represented by nine examples, and if they were correctly identified, and were not a large form of *O. cellarius* (Evans 1972, p. 187) this seems to be the only British subfossil record. Another species about which some doubt exists, is *Cochlodina laminata*, of which single examples were recorded by Kennard & Warren (1903, p. 21) and Woodward (1908, p. 84). All these species were in sand immediately above the 'Head' in what Woodward (1908, p. 14) calls the '*Helix nemoralis* zone' owing to the preponderance of that species, and again there was a sequence of species from those requiring some degree of shade to duneland types. Whimster (1977, p. 71) believes that the presence of woodland species and those intermediate between woodland and drift-soil species in the lower levels at Harlyn 'confirms that the site was covered with scrubby undergrowth in the pre-dune stage.' Assuming that light sand blows preceded the founding of the dunes, increasing the pH, the conditions would have been right for *Pomatias elegans* which today lives at the base of Wild Privet (*Ligustrum vulgare*) at Newquay, adjacent to but not on the dunes.

Gwithian on the east side of the St Ives Bay, is a site showing continuous occupation from Mesolithic times until about 1550 A.D., despite disturbance from the periodic sand blows, the first of which was obvious in Neolithic settlements between 1600 and 1300 B.C. (Thomas 1958). Lewis (1975, p. 159) quotes Thomas (1958 and pers.comm.) as finding *Cochlicella acuta* to have been well established by the beginning of the first millenium B.C., but it was not found at earlier levels where *Cepaea nemoralis* and *Candidula intersecta* were present: this last species is another one believed to have been introduced well within historic times, perhaps since the medieval period (Evans 1972, p. 179). A species provisionally identified as *C. intersecta* has more recently been found at Gwithian by Spencer (1975, p. 100) who places it in a Bronze Age context. However Dr M. P. Kerney (in litt.) thinks that more research is needed before the early arrival of this and other such species in S.W. England can be accepted.



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Spencer (op.cit) also studied the shell sequences of Perranporth dunes and re-examined those of Towan Head, recording a number of species additional to those found under the dunes by previous workers viz. *Carychium tridentatum*, *Cochlicopa lubricella*, *Punctum pygmaeum*, *Vitrina pellucida*, *Vitrea crystallina*, *V. contracta* and *Aegopinella pura*. All these species are catholic in their requirements, and may be broadly termed 'woodland' or shade-loving in contrast to true sand dune species.

Evidence of former coastal woodland comes from the submerged forests around the British Isles, and Ussher (1879, pp. 32–34) summarises the many reports for Cornwall. Deposits in Mount's Bay were dated as 2,000 B.C., using  $^{14}\text{C}$  (de Beer 1962) and thus the beginning of dune formation and the submergence of the forests are closely correlated. It is significant that de Beer (op. cit.) found a great preponderance of alder over oak, supporting the theory of Ussher (1879, p. 45) that drainage was blocked by sand incursions, creating unfavourable conditions for such trees as oak, hazel and birch. Throughout Neolithic times there must have been dramatic coastal changes with valley woodlands being inundated and the inland vegetation, as Evans (1977, p. 22) surmises, increasingly coming under the inimical influence of blown sand, salt-laden winds and the activities of man and his animals.

All this is relevant to the history of the molluscan fauna which, in turn, helps to throw light on former climatic and ecological conditions. Thomas (1958, p. 34) draws attention to the massive sand movements which were first noticed in stratigraphical relationship to one another as Gwithian as human settlements were overwhelmed; sand movements may continue for as long as two centuries before there is a period of stability, marked by a layer of humus where vegetation has 'fixed' the dunes. Both Thomas (1958) and Lennon (1975) record data relating to the cyclic nature of sand blows, the latest of which started about 1935 and is still in progress, causing problems of silting, erosion and inundation. If a reliable chronology of these movements can be worked out, the dating of layers and their fauna, even in the absence of human artifacts, will be feasible.

## THE STUDY OF CORNISH NON-MARINE MOLLUSCA

The influence of the Conchological Society has been even greater on the study of the non-marine Mollusca of Cornwall than it has been on marine studies, to judge by the high proportion of members who have lived in or visited the county, publishing papers and notes, and/or submitting records for the Society's Census: during the past two centuries close on 100 individuals have made such contributions and over 60 (out of 90 who have been active since the inception of the Conchological Society) have been members. Of the 100, 29 have been domiciled in Cornwall for a number of years, 13 of them being Cornish. There has been no steady increase of professional involvement, as with marine Mollusca, although during the past couple of decades, Cornish snails (*Theba pisana* and *Cepaea nemoralis*) have been the subject of half a dozen theses and dissertations. *Lymnaea truncatula*, intermediate host of the liver fluke, concerns MAFF Veterinary Investigation Centres in Cornwall as elsewhere, and these veterinarians have recently had reason to be concerned with certain slugs in the county. This has arisen since the first occurrence in this country (in Cornwall in 1979) of a canine disease caused by the nematode *Angiostrongylus vasorum* and carried by *Arion ater* agg. It is otherwise known only from France (where a number of slug species act as vectors), Italy and Ireland (Jones *et al.* 1980, Simpson & Neal 1982).

There is still much research to be undertaken, particularly on the history of Cornish dune species, and doubtless there are still additions to be made to the county list. Four of the seven species which Woodward (1906, p. 160) thought were recorded in error, have since been authenticated by the Conchological Society's non-marine Recorders; so it may yet be that



some of the doubtful or possibly extinct species to which I have drawn attention in my Address, will be found or re-found.

## ACKNOWLEDGEMENTS

Special thanks are due to Mrs Jean A. Paton whose assiduous collecting in the 1960s did so much to extend our knowledge of Cornwall's non-marine molluscan fauna. I am also grateful to Mr John Humphreys for much helpful information, and to Mrs Patricia A. Burton for re-drawing the map.

ANNOTATED LIST OF CORNISH NON-MARINE MOLLUSCA<sup>1</sup>

<i>Valvata cristata</i> Müller	2 (1) Bude Canal.
<i>V. piscinalis</i> (Müller)	1 (1) pre-1900, Falmouth.
<i>Pomatias elegans</i> (Müller)	1 (4); 2 (2).
<i>Potamopyrgus jenkinsi</i> (Smith)	Abundant.
<i>Hydrobia ulvae</i> (Pennant)	Abundant locally, mainly 2.
<i>Bithynia tentaculata</i> (L.)	1 (1) pre-1900, near Truro. A hard-water species.
<i>Acicula fusca</i> (Montagu)	1 (4); 2 (2).
<i>Carychium minimum</i> Müller	1; 2 Common.
<i>C. tridentatum</i> (Risso)	1; 2 Common.
<i>Ovatella myositis</i> (Draparnaud)	Local.
<i>Leucophytia bidentata</i> (Montagu)	Local.
<i>Aplexa hypnorum</i> (L.)	1 (1) 1840's and c.1914, Falmouth.
<i>Physa fontinalis</i> (L.)	1 (2) 1840's and 1972. Hard-water species; these may have been short-term introductions.
<i>P. cf. acuta</i> Draparnaud	1 (1) 1970's.
<i>P. cf. heterostropha</i> Say	1 (2) 1963 and 1971.
<i>Lymnaea truncatula</i> (Müller)	Abundant.
<i>L. glabra</i> (Müller)	1; 2 Common locally.
<i>L. palustris</i> (Müller)	1; 2 Very local: large <i>L. truncatula</i> have been mistaken for this species.
<i>L. stagnalis</i> (L.)	1 (2) Hard-water species, usually in artificial pools.
<i>L. auricularia</i> (L.)	2 (1) Hard water species: found in Bude Canal in 1983.
<i>L. peregra</i> (Müller)	Abundant. Form <i>ovata</i> Draparnaud in ornamental pools.
<i>Planorbis planorbis</i> (L.)	1 (1) 1840's Falmouth. Hard-water species—could be wrongly identified.

<sup>1</sup>Unless otherwise specified, a species has been recorded in vice-county 1 (West Cornwall), vice-county 1a (Isles of Scilly) and vice-county 2 (East Cornwall). For a rare species, the number of 10 km squares in which it has been found is in brackets following the vice-county number. Nomenclature follows Kerney (1976) and Waldén (1976)



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<i>Anisus leucostoma</i> (Millet)	Abundant, especially in 1.
<i>A. vortex</i> (L.)	1 (3); 1a (1); 2 (1). There is doubt about the authenticity of these records.
<i>Bathyomphalus contortus</i> (L.)	1 (1) 1840's; 2 (1) 1966.
<i>Gyraulus laevis</i> (Alder)	1 (1) 1840's; 2 (2) 1880's and 1937.
<i>G. albus</i> (Müller)	1; 2 Common.
<i>Armiger crista</i> (L.)	1 (only 1 post-1950); 2 (3) pre-1950.
<i>Hippeutis complanatus</i> (L.)	1 (1) c.1914 & 1980; 2 (1) 1966.
<i>Planorbarius corneus</i> (L.)	1 (1) Unpigmented form in quarry. Hard-water species.
<i>Ancylus fluviatilis</i> Müller	1; 2 Common.
<i>Acroloxus lacustris</i> (L.)	1 (1) 1840's. Could be wrongly identified.
<i>Succinea putris</i> (L.)	1; 2 Uncommon.
<i>Oxyloma pfeifferi</i> (Rossmässler)	Common.
<i>Azeca goodalli</i> (Férussac)	1 (1) c.1980 Truro. Calcicole.
<i>Cochlicopa lubrica</i> (Müller)	Common.
<i>C. lubricella</i> (Porro)	Common, but mainly coastal.
<i>Pyramidula rupestris</i> (Draparnaud)	1 (1) 1886; 2 (3) 1887, 1909 and 'early 20th C.'
<i>Columella edentula</i> (Draparnaud) agg.	Fairly common.
<i>C. edentula</i> (Draparnaud) seg.	2 (3)
<i>C. aspera</i> Waldén	1a (1); 1 (2). Tolerates poor acid soils, so likely to be common.
<i>Vertigo antivertigo</i> (Draparnaud)	1 (4); 2 (2) pre-1950.
<i>V. substriata</i> (Jeffreys)	1 (1) Subfossil; 2 1845, 1958 & 1967.
<i>V. pygmaea</i> (Draparnaud)	Fairly common.
<i>Abida secale</i> (Draparnaud)	1 (1) c.1910. Falmouth.
<i>Pupilla muscorum</i> (L.)	1; 2 Common on coast, mainly dunes.
<i>Leiostyla anglica</i> (Wood)	Local.
<i>Lauria cylindracea</i> (da Costa)	Abundant.
<i>Vallonia costata</i> (Müller)	1 (3); 2 (3).
<i>V. excentrica</i> Sterki	Common, especially coastal, on dunes.
<i>Acanthinula aculeata</i> (Müller)	1; 2 Common.
<i>Ena obscura</i> (Müller)	1; 2 Local.
<i>Punctum pygmaeum</i> (Draparnaud)	1; 2 Common.
<i>Discus rotundatus</i> (Müller)	Abundant.
<i>Arion ater</i> (L.) agg.	Abundant. Wild and cultivated places.
<i>A. lusitanicus</i> agg.	Abundant. Wild and cultivated places.
<i>A. subfuscus</i> (Draparnaud)	Common.
<i>A. circumscriptus</i> Johnston agg.	Very common.
<i>A. circumscriptus</i> Johnston seg.	1 (3); 2 (1).
<i>A. silvaticus</i> Lohmander	2 (3).
<i>A. hortensis</i> Férussac agg.	Abundant.
<i>A. hortensis</i> Férussac seg.	1; & 2 Widespread
<i>A. distinctus</i> Mabilie	1; & 2 Widespread
<i>A. owenii</i> Davies	1 (1)
<i>Arion intermedius</i> Normand	Abundant.
<i>Vitrina pellucida</i> (Müller)	Abundant.
<i>Phenacolimax major</i> (Férussac)	1 (1) Shell only; 2 (1).
<i>Vitrea crystallina</i> (Müller) seg.	Abundant.
<i>V. contracta</i> (Westerlund)	Common, but mainly coastal.



<i>Nesovitrea hammonis</i> (Ström)	Widespread but not common.
<i>Aegopinella pura</i> (Alder)	1; 2 Widespread but not very common.
<i>A. nitidula</i> (Draparnaud)	Abundant.
<i>Oxychilus draparnaudi</i> (Beck)	Fairly common, and mainly in gardens.
<i>O. cellarius</i> (Müller)	Abundant.
<i>O. alliarius</i> (Miller)	Abundant.
<i>O. helveticus</i> (Blum)	Abundant.
<i>Zonitoides excavatus</i> (Alder)	1; 2 Common.
<i>Z. nitidus</i> (Müller)	1; 2 Common.
<i>Milax gagates</i> (Draparnaud)	Common.
<i>M. sowerbyi</i> (Férussac)	Common.
<i>M. budapestensis</i> (Hazay)	1; 2 Common.
<i>Boettgerilla pallens</i> Simroth	1; 2 Several sites, and spreading.
<i>Limax maximus</i> L.	Common.
<i>L. cinereoniger</i> Wolf	2 (3) Rare, in old wooded valleys.
<i>L. flavus</i> L. agg.	Fairly common, mainly in and near old buildings.
<i>L. marginatus</i> Müller	Common.
<i>Deroceras laeve</i> (Müller)	Probably common, but under-recorded.
<i>D. caruanae</i> (Pollonera)	Abundant.
<i>D. reticulatum</i> (Müller)	Abundant.
<i>Euconulus fulvus</i> (Müller) agg.	Common.
<i>Ceciloides acicula</i> (Müller)	2 (2) 1916 and c.1970.
<i>Clausilia bidentata</i> (Ström)	1; 2 Abundant.
<i>Balea perversa</i> (L.)	Abundant.
<i>Testacella maugei</i> Férussac	Not uncommon.
<i>T. haliotideae</i> Draparnaud	1 (1) 1880s.
<i>T. scutulum</i> Sowerby	1 (1) 1981.
<i>Candidula intersecta</i> (Poiret)	Common.
<i>Cernuella virgata</i> (da Costa)	Abundant, but mainly coastal.
<i>Helicella itala</i> (L.)	1 Locally common; 1a one 19th C. record; 2 few records. Probably decreasing in county <i>fide</i> J. Humphreys.
<i>Cochicella acuta</i> (Müller)	Abundant on coast.
<i>Monacha cartusiana</i> (Müller)	1 (1) Specimens purported to be from Penzance are in the R. D. Darbishire Coll. ( <i>J. Conch.</i> <b>24</b> , (1956) p. 151) but it is likely that there has been a mix up of labels.
<i>Monacha cantiana</i> (Montagu)	1 (1) pre-1950 record from dunes; 2 (2) one pre-1950 record from dunes and one 1967 record from limestone near Plymouth.
<i>Ashfordia granulata</i> (Alder)	Abundant.
<i>Zenobiella subrufescens</i> (Miller)	1 Rather local; 2 Rather local.
<i>Trichia striolata</i> (Pfeiffer)	Abundant.
<i>T. hispida</i> (L.)	Abundant.
<i>Pomentina subvirescens</i> (Bellamy)	Locally common on coast, and very occasionally more inland.
<i>Arianta arbustorum</i> (L.)	1 rare; 2 very local.



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<i>Theba pisana</i> (Müller)	1 (5) Three sites extinct, and two remaining.
<i>Cepaea nemoralis</i> (L.)	Abundant.
<i>C. hortensis</i> (Müller)	1 uncommon; 2 not very common.
<i>Helix aspersa</i> Müller	Abundant. In wild and cultivated places
<i>Margaritifera margaritifera</i> (L.)	2 (2) Soft-water species.
<i>Anodonta anatina</i> (L.)	2 (2) Hard-water species.
<i>Sphaerium lacustre</i> (Müller)	1 (2); 2 (5).
<i>Pisidium amnicum</i> (Müller)	2 (2). Early records for v-c 1 are probably erroneous.
<i>P. casertanum</i> (Poli)	Abundant.
<i>P. personatum</i> Malm	Common.
<i>P. obtusale</i> (Lamarck)	Local.
<i>P. milium</i> Held	Local.
<i>P. subtruncatum</i> Malm	Local.
<i>P. henslowanum</i> (Sheppard)	1 (1) c.1910; 2 (2).
<i>P. hibernicum</i> Westerlund	1 (1)
<i>P. nitidum</i> Jenyns	1; 2 Local.
<i>P. moitessierianum</i> Paladilhe	2 (2).
<i>Dreissena polymorpha</i> (Pallas)	1 (1) One shell by R. Hayle in 1977 with fresh remains of dead animal.

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# SEPTIBRANCHES ABYSSAUX DE L'Océan INDIEN OCCIDENTAL (MOLLUSQUES BIVALVES ANOMALODESMATA)

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**Abstract:** The present paper deals with 14 species of abyssal Septibranchs, of which 4 species and 1 subspecies are described as new. Two species (*Cuspidaria undata*, *Cetoconcha* sp. 2) have been trawled at 3825–4035 m, in the W. Madagascar basin, by the oceanographic cruise 'Safari MD 20', 1979. The other species were collected during the 'Benthedi' expedition, 1977, in the North of Moçambique channel, at 3450–3716 m depth. Among these last species, some have already been recorded from the Atlantic Ocean (*Poromya tornata*, *Cetoconcha transversa*, *Cuspidaria barnardi*, *Lyonsiella* cf. *formosa*); other ones are known only from the Indian Ocean (*Cuspidaria benthedii* n.sp., *Myonera angularis quadrostrata* n.ssp., *Protocuspidaria thomassini* n.sp., *Verticordia excoriata* n.sp., *Lyonsiella curta* n.sp., *Lyonsiella galathea*); two others have not been identified (*Cetoconcha* sp. 1, *Cuspidaria* sp.). This work provides illustrations for every species and, as much as possible, considers the main anatomical characters of the different species. This is the first Indian Ocean record for genus *Protocuspidaria*. The type material of the new forms described in this paper is kept in the Museum national d'Histoire naturelle, Paris.

**Résumé:** Le présent rapport concerne 14 espèces de Septibranches abyssaux, parmi lesquelles 4 espèces et 1 sous-espèce sont nouvelles. Deux espèces (*Cuspidaria undata* et *Cetoconcha* sp. 2) ont été recueillies à 3825–4035 m, dans l'ouest du bassin de Madagascar, par la mission océanographique 'Safari MD 20' de 1979. Les autres espèces ont été récoltées lors de la campagne 'Benthedi' de 1977, au nord du canal de Mozambique, par 3450–3716 m de fond. Parmi ces dernières espèces, certaines sont connues de l'océan Atlantique (*Poromya tornata*, *Cetoconcha transversa*, *Cuspidaria barnardi*, *Lyonsiella* cf. *formosa*); d'autres n'ont été trouvées que dans l'océan Indien (*Cuspidaria benthedii* n.sp., *Myonera angularis quadrostrata* n.ssp., *Protocuspidaria thomassini* n.sp., *Verticordia excoriata* n.sp., *Lyonsiella curta* n.sp., *Lyonsiella galathea*); deux formes n'ont pas reçu d'attribution spécifique (*Cetoconcha* sp. 1, *Cuspidaria* sp.). On a tenu compte, dans la mesure du possible, des caractères anatomiques principaux des différentes espèces qui ont toutes été illustrées. Le genre *Protocuspidaria* est ici cité pour la première fois de l'océan Indien.

## INTRODUCTION

Les Bivalves abyssaux mentionnés dans ce travail proviennent surtout des récoltes réalisées dans le nord du canal de Mozambique par la mission Benthedi en mars-avril 1977. Lors de cette campagne de recherches, effectuée sous la direction de Mr B. Thomassin par le navire océanographique 'Suroît', avec Mr Ph. Bouchet comme malacologiste à bord, trois stations de chalutages profonds ont fourni des Septibranches en quantités appréciables.

On y a adjoint les quelques spécimens rapportés de l'ouest du bassin de Madagascar par la campagne Safari MD 20 en août-septembre 1979. Les chalutages profonds, réalisés sous la direction de Mr Cl. Monniot par le MS 'Marion-Dufresne', n'ont livré que dans deux stations des Septibranches (ne représentant qu'une faible proportion des Bivalves récoltés).

L'ensemble du matériel étudié comprend 14 espèces dont 4 espèces et 1 sous-espèce sont nouvelles pour la Science. Les types de ces formes nouvelles ont été déposés au laboratoire de Malacologie du Muséum national d'Histoire naturelle (MNHN) de Paris.

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Pour chaque espèce, on s'est attaché à donner une illustration des spécimens récoltés, une synonymie condensée, les coordonnées géographiques moyennes des récoltes, des indications sur la distribution géographique et bathymétrique, et des remarques sur divers problèmes apparus lors de l'étude du matériel. On a aussi, toutes les fois que cela a paru possible ou souhaitable, décrit les caractères principaux des parties molles.

Je tiens à remercier ici MM. B. Thomassin, Cl. Monniot et Ph. Bouchet, pour m'avoir confié cet intéressant matériel, qui a été en grande partie trié par le Centob à Brest; Mr Cl. Lévi, pour m'avoir accueilli dans son laboratoire de Biologie des Invertébrés marins du Muséum d'Histoire naturelle de Paris; Mr T. Okutani, du National Science Museum de Tokyo, pour avoir répondu à mes demandes de matériel et de documentation; Mr A. Foubert, du laboratoire de Malacologie du Muséum de Paris, pour les clichés photographiques; Mme D. Vukadinovic, pour l'aide précieuse qu'elle m'a apportée grâce à ses connaissances en langue russe.

## ETUDE SYSTEMATIQUE

### POROMYIDAE Dall 1886

**Poromya tornata** (Jeffreys 1876). (pl. 17, Figs. 1–3)

*Pecchiola tornata* Jeffreys 1876, p. 494.

*Poromya tornata* Knudsen 1970, p. 124, Figs. 82–84, pl. 14 Fig. 9; Allen & Morgan 1981, pp. 503–514, Figs. 68–77.

### Matériel

Benthedi St.82, 1.04.77, entre Mayotte et le nord du banc du Geyser, 11°59,8'S, 45°42,6'E, 3450 m: 1 exemplaire vivant.

Benthedi St.87, 3.04.77, sud-est des Glorieuses, 11°44'S, 47°35'E, 3716 m: 1 exemplaire vivant, 1 coquille vide.

Benthedi St.90, 4.04.77, sud-est des Glorieuses, 11°44'S, 47°30'E, 3700 m: 2 exemplaires vivants.

### Remarques

Cette espèce de Jeffreys a été fort bien redéfinie et figurée par Knudsen (op.cit.), en particulier en ce qui concerne l'anatomie des parties molles. L'étude comparée du présent matériel avec des échantillons de *Poromya isocardioides* Dautzenberg & Fischer 1897 dragués dans l'Atlantique par le N. O. Jean Charcot lors de la mission 'Biaçores' en 1971, permet de confirmer l'opinion de Knudsen suivant laquelle cette espèce doit être considérée comme synonyme de *P. tornata*.

### Distribution

*P. tornata* possède une vaste distribution dans l'Atlantique nord et central ainsi que dans l'ouest et le centre de l'océan Indien; elle a été récoltée vivante entre 2940 m (matériel 'Biaçores') et 5300 m.



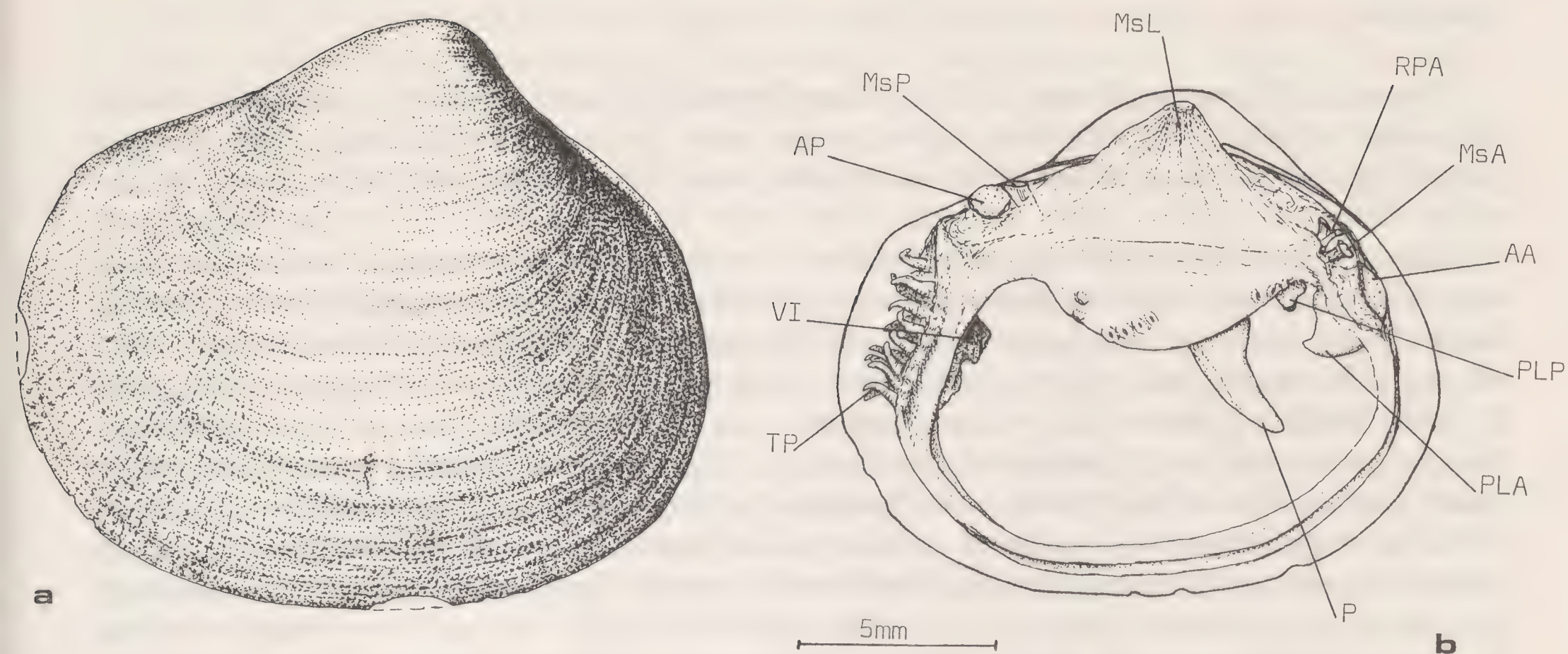


Fig. 1. *Cetoconcha transversa* (Locard). Benthedi St.90: a, valve droite, vue externe, 14,6 mm; b, animal vu du côté droit, valve droite enlevée.

Abbréviations:

AA	adducteur antérieur.	MsP	muscle septal postérieur.
AP	adducteur postérieur.	P	pied.
Br	branchies.	PLA	palpes labiaux antérieurs.
DD	diverticules digestifs.	PLP	palpes labiaux postérieurs.
FBr	fentes branchiales.	Po	pores septaux.
G	gonades.	RPA	rétracteur pédieux antérieur.
GIR	glandes radiales du manteau.	RPP	rétracteur pédieux postérieur.
MaS	manchon siphonal.	SE	siphon exhalant.
ML	muscle longitudinal.	SI	siphon inhalant.
MsA	muscle septal antérieur.	TP	tentacules périssiphonaux.
MsL	muscle septal latéral.	VI	valvule infraseptale.

Nota: Les longueurs en millimètres correspondent à la plus grande dimension de chacun des spécimens figurés.

**Cetoconcha transversa** (Locard 1898). (Fig. 1a–b)

*Verticordia transversa* Locard 1898, p. 201, pl. 10 Figs. 1–4; Clarke 1962, p. 70; Allen & Turner 1974, p. 531.

*Lyonsiella transversa* Nordsieck 1969, p. 167, pl. 23 Fig. 96.01.

*Thracidora transversa* Knudsen 1970, p. 174.

*Matériel*

Benthedi St.87, 3.04.77, sud-est des Glorieuses, 11°44'S, 47°35'E, 3716 m: 1 exemplaire vivant.

Benthedi St.90, 4.04.77, sud-est des Glorieuses, 11°44'S, 47°30'E, 3700 m: 1 exemplaire vivant.

(Expédition du Talisman, St.175 (1883): 1 exemplaire type vivant, à test fragmenté).



*Description*

Largeur 14,6 mm, hauteur 12,4 mm, renflement 9,8 mm (spécimen Benthedi St.90). Coquille subéquivalve, renflée, plus large que haute, inéquilatérale, de contour grossièrement quadrangulaire, à test blanchâtre, mince et translucide, baillant postérieurement. Crochets renflés, assez saillants, situés vers le tiers antérieur du test, dirigés vers l'intérieur et vers l'avant. Bord dorsal antérieur court, oblique, légèrement convexe, tendant à se raccorder anguleusement avec le bord antérieur qui est assez régulièrement arrondi. Bord ventral largement arqué, arrondi postérieurement. Bord postérieur convexe, formant un angle émoussé avec le bord dorsal postérieur qui est long, subrectiligne et faiblement déclive. Surface externe des valves convexe, un peu comprimée postéro-dorsalement, d'aspect lisse et luisant. Une petite ride radiale s'étend le long du bord dorsal postérieur de chaque valve. Valve droite tendant à déborder extérieurement sur l'autre valve au niveau de la marge dorsale du test. Sculpture externe peu saillante, composée de fines stries et lignes concentriques d'accroissement ainsi que de nombreuses lignes rayonnantes de minuscules granulations facilement érodées (cette sculpture radiale tend à être un peu plus accusée dans la région postérieure du test). Périostracum mince, luisant, jaune pâle translucide, s'épaississant un peu à la périphérie des valves. Un léger changement de teinte délimite en avant des crochets une petite lunule dépourvue de granulations.

Ligament externe, jaunâtre, assez saillant, s'insérant en arrière des crochets sur une courte nympe qui renforce un peu le bord cardinal.

Charnière très peu épaisse, complètement dépourvue de dents. Surface interne des valves blanchâtre, devenant nacrée à la périphérie du test, au-delà des impressions musculaires qui apparaissent plus ou moins nettes. Ligne palléale assez large, avec un sinus très peu profond. Empreinte adductrice antérieure ovale, la postérieure subquadratique. Marges internes minces et lisses.

Parties molles: Ouverture pédieuse s'étendant environ sur les trois quarts antérieurs de la marge palléale qui est modérément épaisse. Siphon inhalant à ouverture large, entouré de sept paires de tentacules forts et pointus, prolongé dans la chambre infraseptale par une valvule robuste mais assez courte. Siphon exhalant saillant, surmonté dorsalement par un tentacule analogue à ceux du siphon inhalant. Pied assez grand, avec une petite fente byssale, pourvu de trois muscles rétracteurs bifides. Palpes labiaux dissymétriques, les antérieurs grands et cupuliformes, les postérieurs plus réduits. Septum bien développé, muni de trois paires d'oscles constitués par des pores alignés: chaque oscule antérieur comporte cinq à six pores, entre le pied et les palpes postérieurs; les oscles médians, situés en arrière du pied, comprennent chacun cinq pores, alors qu'il n'y en a que trois par oscule postérieur. Septum prolongé de chaque côté par de longues fibres musculaires qui se renforcent un peu vers l'arrière et convergent dorsalement vers la région umbonale pour constituer un muscle septal latéral. Muscles septaux antérieurs et postérieurs bien développés, l'extrémité de chaque antérieur apparaissant surmontée dorsalement par un muscle rétracteur pédieux bifide (l'extrémité du rétracteur pédieux postérieur, mince et longuement bifide, s'insère dorsalement entre les extrémités de l'adducteur postérieur).

*Remarques*

Les proportions de la coquille de *Cetoconcha transversa* présentent une certaine variabilité, sa forme pouvant être plus ou moins étirée en largeur. En ce qui concerne les parties molles, outre le nombre variable de pores aux oscles septaux antérieurs, on a pu noter la présence d'un tentacule périssiphonal surnuméraire du côté gauche (exemplaire du Talisman).



La position systématique de *C. transversa* a été fort mal interprétée par les différents auteurs qui ont cependant toujours rangé cette espèce parmi les Verticordiidae: c'est ainsi qu'elle a été considérée soit comme une *Verticordia* (s.l.), soit comme une *Lyonsiella* (Nordsieck 1969) à cause de sa forme quadrangulaire, ou encore comme une *Thracidora* (Knudsen 1970), cette dernière opinion se fondant sur les travaux de Thiele (1935, p. 944) et de Soot-Ryen (1966, p. 26) qui proposaient de transférer le genre *Thracidora* des Thraciidae aux Verticordiidae.

L'espèce, qui a été décrite et figurée par Locard (1898) à partir d'un exemplaire entier et de quelques fragments provenant de la st. 175 de l'expédition du Talisman de 1883, ne semble pas avoir été retrouvée depuis. Le matériel de Locard conservé au Muséum national d'Histoire naturelle de Paris est actuellement constitué de fragments de test ainsi que des parties molles d'un individu conservé à sec. L'examen de ces parties molles (ainsi que de la valve gauche, peu fragmentée et qui a pu être reconstituée) a permis de ranger indiscutablement l'espèce de Locard dans le genre *Cetoconcha* et d'établir son identité avec le matériel de Benthedi. On a aussi pu constater que les dimensions de l'exemplaire du Talisman étaient d'environ 25 mm (et non 35) pour la largeur, 17 pour la hauteur, et 15 pour le renflement.

Parmi les autres espèces rapportées au genre *Cetoconcha*, *C. transversa* se distingue de *C. ceylonensis* Knudsen 1970 de l'océan Indien central, par son contour plus allongé et quadrangulaire (bord dorsal antérieur plus court et comme tronqué en avant, bord ventral moins arrondi), ainsi que par ses crochets antérieurs et non submédians.

Par son test, *C. transversa* est morphologiquement proche de '*Cetoconcha*' *malespinae* Dall 1916 du Pacifique oriental dont de bonnes descriptions et illustrations ont été fournies par F. R. Bernard (1974, pp. 81–82, pl. 21 Figs. 1–2); cependant, *C. transversa* peut se reconnaître à sa forme moins globuleuse et plus aplatie ventralement, sa surface interne nacrée à la périphérie, sa charnière dépourvue de tubercule dentiforme à la valve droite. De plus, il faut signaler que la présence de deux paires d'oscles septaux formés de filaments et d'interfilaments permet de rapporter l'espèce de Dall au genre *Poromya* (cf. Ridewood 1903, p. 272, Fig. 58a–d).

La conformation du test permet aussi de reconnaître *C. transversa* de *C. braziliensis* et de *C. angolensis*, récemment décrites de l'Atlantique abyssal par Allen & Morgan (1981, pp. 521–529, Figs. 84–93). En effet, *C. braziliensis* se distingue par son contour ovale subtrigone et non quadrangulaire, par ses rayons granuleux moins nombreux et limités à la déclivité postérieure, et par son empreinte adductrice antérieure beaucoup plus grande que la postérieure. *C. angolensis* diverge de *C. transversa* par ses crochets submédians et non nettement antérieurs, ainsi que par son bord dorsal postérieur plus déclive, ce qui donne au test un aspect faiblement inéquilatéral. De plus, les rétracteurs pédieux antérieurs des deux espèces de Allen & Morgan sont simples et non bifides.

### *Distribution*

Cette espèce a été récoltée vivante au nord des Açores, par 4165 m de fond (Locard 1898) et au sud-est des îles Glorieuses vers 3700 m (matériel de Benthedi).



**Cetoconcha sp.1***Matériel*

Benthedi St.87, 3.04.77, sud-est des Glorieuses, 11°44'S, 47°35'E, 3716 m: 1 exemplaire vivant, à coquille très fragmentaire.

*Description*

Parties molles: Manteau mince, à ouverture pédieuse s'étendant sur la majeure partie de la marge ventrale qui est fortement épaissie. Siphon inhalant non saillant, à ouverture relativement large, entouré de sept paires de tentacules robustes et pointus, prolongé dans la chambre infraseptale par une valvule robuste qui s'étend vers l'avant sur environ la moitié de la distance séparant le siphon du pied. Siphon exhalant saillant, surmonté dorsalement par un tentacule un peu moins long mais de même forme que les autres tentacules. Pied assez grand, comportant une protubérance basale postérieure, mais dépourvu de sillon byssal. Palpes labiaux dissymétriques: les antérieurs très grands et lamelliformes; les postérieurs beaucoup plus petits, subtrigones. Septum assez musculeux, muni de trois paires d'oscles constitués par des pores alignés: oscles antérieurs comprenant chacun six pores, s'allongeant entre les palpes labiaux et le pied; oscles médians rebordant latéralement la partie postérieure du pied et formés de quatre pores chacun; oscles postérieurs ne comportant chacun que deux pores, situés juste en arrière des oscles médians, mais en position très latérale par rapport à ceux-ci.

*Remarques*

L'exemplaire décrit ci-dessus ne possédant que quelques débris de test (zone postérieure essentiellement), il n'a pas été possible de procéder de manière satisfaisante à son identification spécifique. Toutefois, la présence de trois paires d'oscles septaux le rattache indiscutablement au genre *Cetoconcha* Dall 1886 (il en va de même pour le matériel de la st.15 CP 08 de Safari mentionné ci-après).

**Cetoconcha sp.2***Matériel*

Safari St.15 CP 08, 2.09.79, ouest du Bassin de Madagascar, 31°51,8'S, 48°28,8'E, 3825 m: 2 exemplaires vivants, fortement endommagés.

*Remarques*

Les spécimens de la st.15 CP 08 n'ont pu être déterminés spécifiquement à cause de leur médiocre état de conservation: ils ne présentent en effet que des parties molles endommagées et fortement contractées associées à quelques débris de coquille. On a pu noter les caractères communs suivants:



Manteau mince et translucide, à marge ventrale fortement épaissie et munie d'une ouverture pédieuse dépassant la moitié de sa longueur. Tentacules périssiphonaux robustes et pointus, huit de chaque côté du siphon inhalant et un dorsalement au siphon exhalant. Valvule infraseptale assez grande. Pied épais et conique, avec une protubérance basale postérieure. Palpes labiaux très dissymétriques: les antérieurs très grands, lamelliformes et repliés en deux longitudinalement; les postérieurs bien plus réduits, subtrigones. Septum épais, muni de trois paires d'oscles constitués par des pores alignés.

Cependant, les deux spécimens présentant certaines différences (en particulier la couleur de leurs parties molles, blanchâtre pour l'un, rosée pour l'autre), il se peut qu'ils correspondent à des formes distinctes; en effet, chez le spécimen 'rose', l'ouverture pédieuse apparaît un peu moins étendue, le pied muni d'une mince fente byssale, et les oscles septaux constitués respectivement de six pores pour les antérieurs, six pour les médians et trois pour les postérieurs; par contre, chaque oscule du spécimen 'blanc' comprend six pores, sauf l'osculé postérieur droit qui n'en a que quatre.

CUSPIDARIIDAE Dall 1886

**Cuspidaria barnardi** Knudsen 1970. (pl. 17, Fig. 4)

*Cuspidaria barnardi* Knudsen 1970, p. 139, Figs. 96–97; Allen & Morgan 1981, p. 457, Fig. 24.

#### *Matériel*

Benthedi St.87, 3.04.77, sud-est des Glorieuses, 11°44'S, 47°35'E, 3716 m: 1 exemplaire vivant (valve droite endommagée).

#### *Remarques*

On peut distinguer quelques faibles lignes rayonnantes à l'extrémité postérieure du rostre de l'exemplaire de la st.87 qui, par ailleurs, correspond bien aux descriptions et illustrations données par Knudsen (op.cit.).

#### *Distribution*

Cette espèce est connue de l'océan Indien par le présent matériel et par l'holotype de Knudsen, dragué au sud-est de l'Afrique à 3530 m de profondeur. D'après Allen & Morgan (1981), elle aurait aussi une vaste distribution dans l'océan Atlantique où elle a été récoltée vivante entre 2178 et 3828 m.

**Cuspidaria undata** (Verrill 1884). (Fig. 2a–b; pl. 17, Figs. 5–7)

*Neaera undata* Verrill 1884, p. 223.

*Cuspidaria undata* Verrill & Bush 1898, p. 798, pl. 72 Fig. 1, pl. 78 Figs. 3–4; Allen & Morgan 1981, p. 458.

*Myonera undata* Knudsen 1970, p. 136, Figs. 93–94.



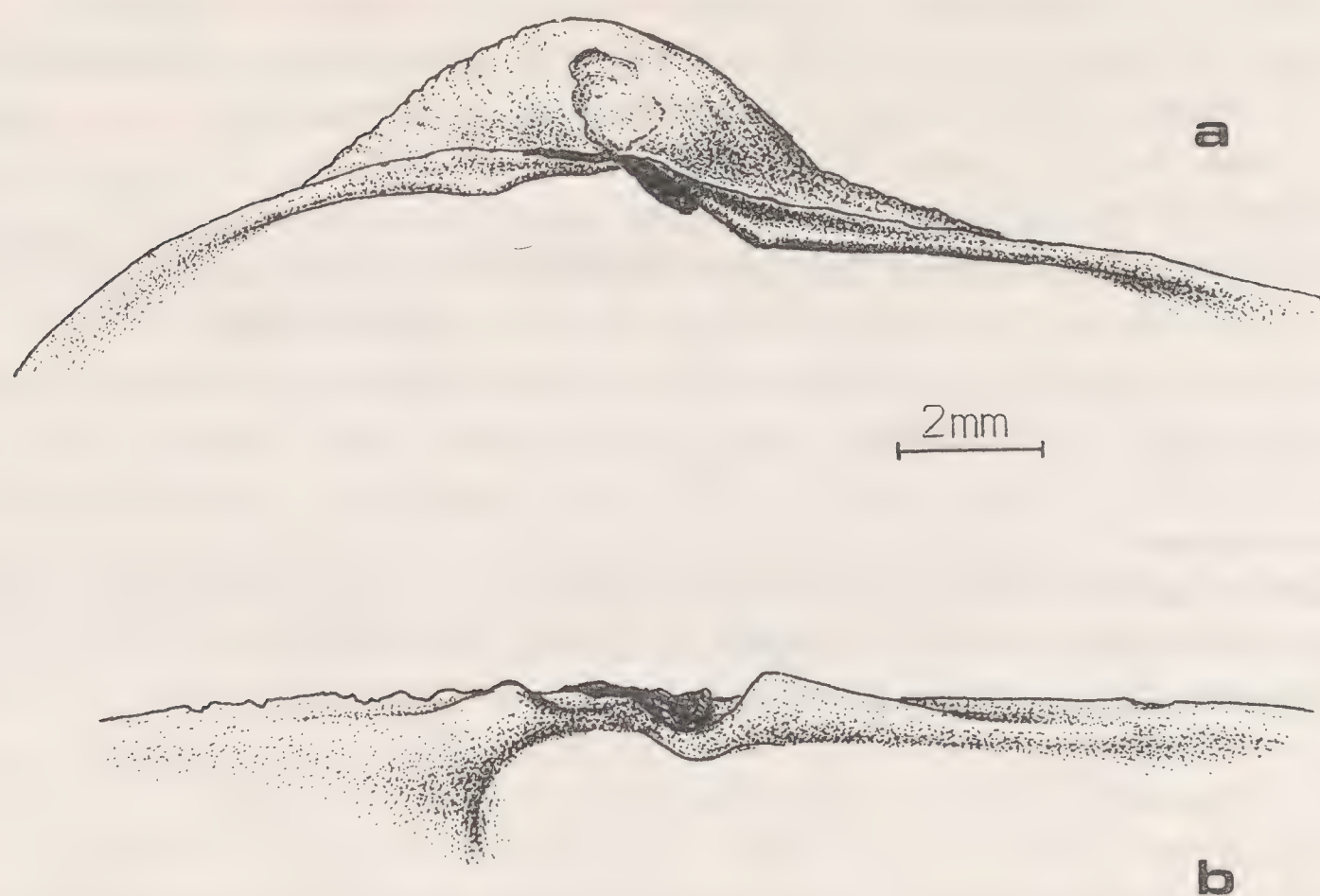


Fig. 2. *Cuspidaria undata* (Verrill). Safari St.11 CP 06: a-b, charnière de la valve droite, vues interne et ventrale.

### Matériel

Safari St.11 CP 06, 31.08.79, ouest du Bassin de Madagascar, 30°39,9'S, 48°14,5'E, 4020–4035 m: 2 exemplaires vivants (dont l'un est très fragmentaire).

### Remarques

Le présent matériel correspond tout à fait à l'excellente définition que donne Knudsen (1970) de '*Myonera*' *undata*. Cependant, la charnière de cette espèce n'étant pas édentule, il y a lieu de la considérer comme une *Cuspidaria*, malgré une ressemblance superficielle avec certaines *Myonera* à côtes.

Contrairement à ce qu'affirment Allen & Morgan (1981, p. 459), la charnière de la valve droite possède bien une petite dent antérieure en plus de la forte dent postérieure. Ce dentelon antérieur, bien visible sur le spécimen intact de Safari avait déjà été noté et même figuré (quoique peu distinctement) par Knudsen (op.cit., p. 137, Fig. 94a).

### Distribution

*C. undata* possède une vaste distribution dans les océans Atlantique et Indien dans lesquels elle a été récoltée vivante entre 4020 m (présent matériel) et 5300 m.



**Cuspidaria benthedii** n.sp. (Fig. 3a-e)*Matériel*

Benthedi St.87, 3.04.77, sud-est des Glorieuses, 11°44'S, 47°35'E, 3716 m: 208 exemplaires vivants (holotype et paratypes).

Benthedi St.90, 4.04.77, sud-est des Glorieuses, 11°44'S, 47°30'E 3700 m: 7 exemplaires vivants (paratypes).

Holotype: MNHN.

*Description*

Largeur 3,2 mm, hauteur 1,8 mm, renflement 1,1 mm (holotype). Coquille modérément renflée, atteignant 3,2 mm de long, légèrement inéquivalve (la valve gauche débordant ventralement de l'autre valve), inéquilatérale, à test blanchâtre et mince. Contour pyriforme, allongé transversalement, à côté postérieur étiré en forme de rostre. Crochets assez saillants, situés au tiers antérieur de la largeur des valves. Bord dorsal antérieur décline et doucement convexe, se raccordant sans discontinuité marquée avec le bord antérieur qui est régulièrement arrondi. Bord ventral largement arqué, devenant subconcave postérieurement. Rostre relativement large, mal délimité par rapport au reste de la coquille, subtrigone et tronqué à l'extrémité postérieure. Sculpture externe de chaque valve composée d'une dizaine de côtes concentriques auxquelles se superposent de légères et nombreuses marques d'accroissement; côtes concentriques étroites et espacées, s'affaiblissant dans la région umbonale et tendant à former de fines lamelles ventralement, limitées vers l'arrière par une ride rayonnant du crochet à l'extrémité postéro-ventrale du rostre. Périostracum adhérent, beige translucide, devenant plus sombre et fibreux à la périphérie des valves où il rehausse les marques de croissance du test (surtout ventralement et postérieurement).

Ligament interne brun-corné, s'insérant à chaque valve dans une petite fossette située au-dessous du crochet et non saillante ventralement.

Charnière dépourvue de dents à la valve gauche, mais comportant à la valve droite deux dents bien développées dont la postérieure est la plus courte. Surface interne du test marquée de faibles ondulations concentriques correspondant à la sculpture externe. Impressions musculaires peu visibles. Marges internes lisses.

Parties molles: Ouverture pédieuse limitée à la région antérieure de la marge palléale qui est assez épaisse. Manchon siphonal allongé, un peu épaissi et ridé intérieurement à son extrémité postérieure qui est prolongée, le long de chaque valve, par un revêtement périostracal. Siphon inhalant large et robuste, beaucoup plus volumineux que le siphon exhalant. Siphons entourés par sept tentacules filiformes (quatre ventralement autour du siphon inhalant, et trois dorsalement autour du siphon exhalant). Ouverture inhalante débouchant dans la chambre infraseptale par une valvule munie en son milieu d'une fente verticale. Pied long et cylindrique, renflé à la base, avec une longue fente byssale sur sa face postérieure, muni de trois muscles rétracteurs: le rétracteur pédieux postérieur mince et allongé, largement bifide; les rétracteurs antérieurs plus courts et plus épais. Palpes labiaux très petits, s'insérant sur un léger bourrelet limitant extérieurement l'entonnoir buccal: palpes antérieurs digitiformes, écartés l'un de l'autre et de l'ouverture buccale; palpes postérieurs réduits à de simples protubérances juxtaposées (type I de Allen & Morgan 1981). Septum épais, fortement strié longitudinalement, à pores indistincts; muscles septaux antérieurs bifides, les postérieurs simples.



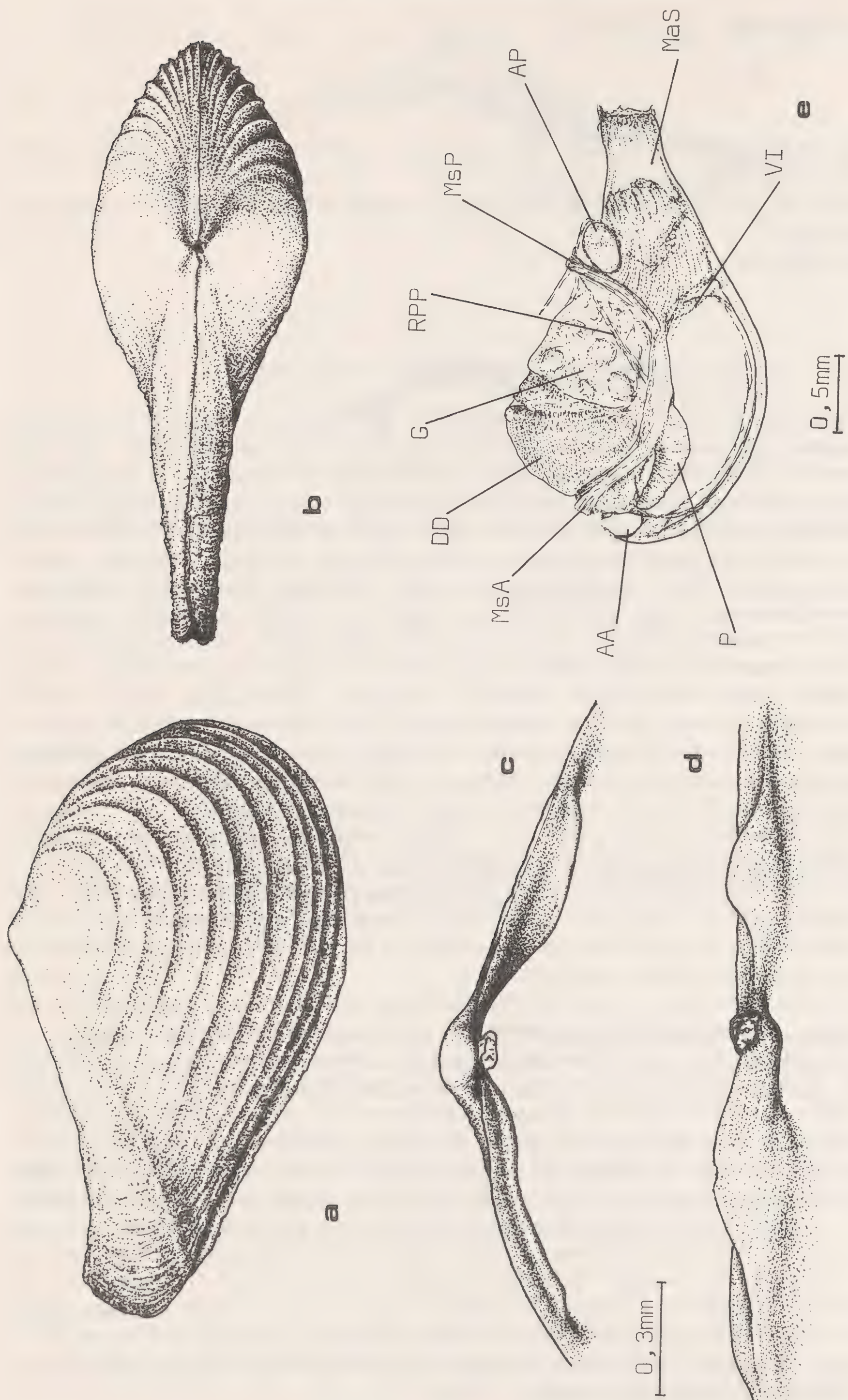


Fig. 3. *Cuspidaria benthedii* n.sp. Benthedi St.87: a-b, vues externes du test, côté droit et vue dorsale; c-d, charnière de la valve droite, vues interne et ventrale; e, parties molles, vues du côté gauche (a-b, holotype, 3,2 mm; c-e, paratypes).



*Remarques*

Cette espèce, qui ressemble quelque peu à *C. murrayi* (Smith 1885) du Pacifique central, s'en distingue cependant par sa forme moins allongée, ses crochets plus saillants et situés plus en avant, son rostre moins gracile et ses côtes concentriques moins serrées. Enfin, *C. benthedii* présente deux dents bien développées à la valve droite, alors que la charnière de *C. murrayi* est complètement édentule. Cette conformation de la charnière permet aussi de distinguer aisément *C. benthedii* de *C. atlantica* Allen & Morgan 1981 du bathyal de l'océan Atlantique, de *C. rara* Thiele 1931 et de *C. agulhasensis* Thiele 1931 de l'océan Indien occidental, qui ne possèdent qu'une dent postérieure à la valve droite (d'après Barnard 1964 ces deux dernières espèces représenteraient des exemplaires juvéniles de *C. optima* Sowerby 1904).

Par sa charnière dépourvue de dents à la valve gauche, mais possédant à la valve droite une dent latérale antérieure et une postérieure, *C. benthedii* correspond au sous-genre *Rhinoclama* Dall & Smith 1886 (in Dall 1886, p. 300) tel que l'ont redéfini Allen & Morgan (1981, pp. 423, 428, 479).

*Distribution*

*C. benthedii* a été récoltée en abondance au sud-est des îles Glorieuses où elle vit vers 3700 m de profondeur.

**Cuspidaria sp. (Fig. 4)***Matériel*

Benthedi St.90, 4.04.77, sud-est des Glorieuses, 11°44'S, 47°30'E, 3700 m: 2 exemplaires vivants, à test endommagé.

*Remarques*

Etant donné le relativement mauvais état du test des deux exemplaires disponibles, cette espèce ne sera pas nommée. Elle se rapproche de *Cuspidaria murrayi* (Smith 1885) du Pacifique central, par son aspect général allongé et son rostre mal délimité par rapport au reste du test. Cependant, elle s'en distingue nettement par un rapport hauteur/largeur plus important, par

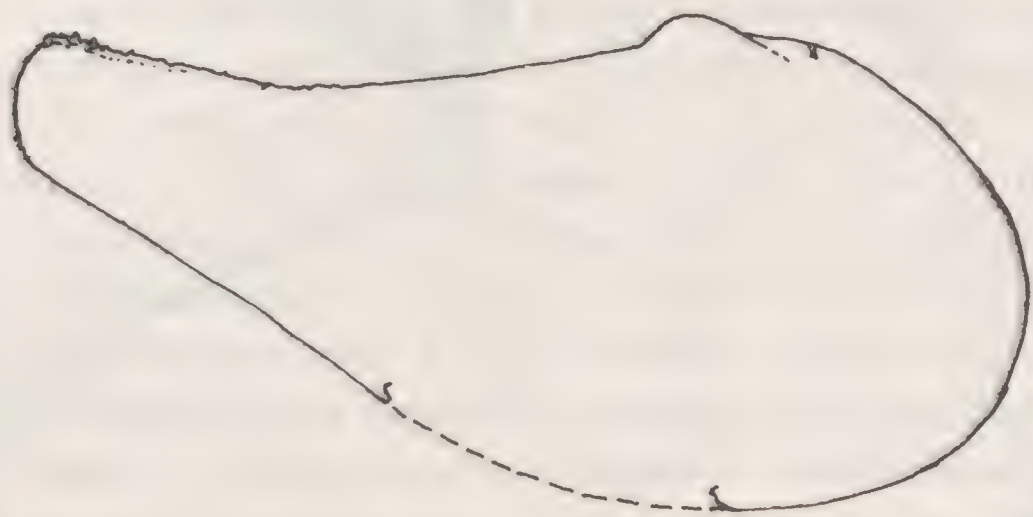


Fig. 4. *Cuspidaria* sp. Benthedi St.90: contour schématique externe de la valve droite, 8 mm.



ses crochets plus antérieurs et un peu plus saillants, ainsi que par sa charnière non complètement édentule. Elle s'écarte de *C. benthedii* par sa plus forte taille (8 mm de large chez le plus grand exemplaire), ses côtes concentriques plus nombreuses, son rostre nettement concave dorsalement et orné de cordonnets radiaux irréguliers en plus de la sculpture concentrique, et par sa charnière ne comportant qu'une faible dent postérieure à la valve droite.

***Myonera angularis quadrostrata* n.ssp. (Fig. 5a–c)**

*Neaera angularis* Jeffreys 1876, pp. 498–499; Jeffreys 1881, p. 943, pl. 71 Fig. 9.

*Myonera angularis* Nordsieck 1969, p. 172.

*Matériel*

Benthedi St.87, 3.04.77, sud-est des Glorieuses, 11°44'S, 47°35'E, 3716 m: 1 exemplaire vivant (holotype) et 5 exemplaires vivants à coquilles endommagées (paratypes).

Benthedi St.90, 4.04.77, sud-est des Glorieuses, 11°44'S, 47°30'E, 3700 m: 1 exemplaire vivant (paratype).

Holotype: MNHN.

*Description*

Largeur 3,9 mm, hauteur 3,2 mm, renflement 2,6 mm (holotype). Coquille renflée, atteignant 5,6 mm de long, presque équivalve (la valve gauche débordant légèrement de l'autre valve ventralement et postérieurement), inéquilatérale, à test blanchâtre et fragile. Contour largement arrondi dans sa moitié antérieure, et dont la moitié postérieure est étirée en un rostre baillant et tronqué en arrière. Crochets assez grands et arrondis, dirigés vers l'intérieur, situés en avant de la ligne médiane des valves (la zone post-umbonale forme environ 60% de la longueur totale). Surface externe des valves convexe, devenant déprimée postérieurement dans une zone comprise entre deux côtes radiales qui déterminent chacune une angulosité à la marge des valves; ces côtes rayonnent de la région umbonale à l'extrémité postéro-ventrale du test pour la plus dorsale, et au tiers postérieur du bord ventral pour la plus ventrale qui est aussi la plus forte. En avant de cette côte umbono-ventrale, la sculpture externe est composée d'une vingtaine de côtes concentriques arrondies et assez régulièrement espacées, devenant progressivement indistinctes dans la région umbonale. Entre la côte umbono-postérieure et la marge dorsale postérieure du test, la surface du rostre montre environ quatre cordonnets rayonnants, croisés de nombreuses stries et lignes transverses irrégulières et serrées. Dans la zone comprise entre les deux côtes radiales, on observe une sculpture 'intermédiaire' entre celles des zones voisines, avec de faibles ondulations concentriques vers l'avant et une striation très fine, irrégulière et serrée vers l'arrière.

Ligament interne brun-corné, grossièrement trigone, dirigé obliquement vers l'arrière.

Charnière des deux valves dépourvue de dents, à bord cardinal légèrement épaissi intérieurement sauf à l'aplomb des crochets où il est échancré par une petite fossette résilifère. Surface interne blanche et luisante, laissant transparaître la sculpture externe. Impressions musculaires indistinctes. Marges internes minces et lisses.

Parties molles: Manteau mince et translucide, ouverture pédieuse s'étendant sur environ la moitié de la marge palléale qui est relativement épaisse. Manchon siphonal simple, un peu



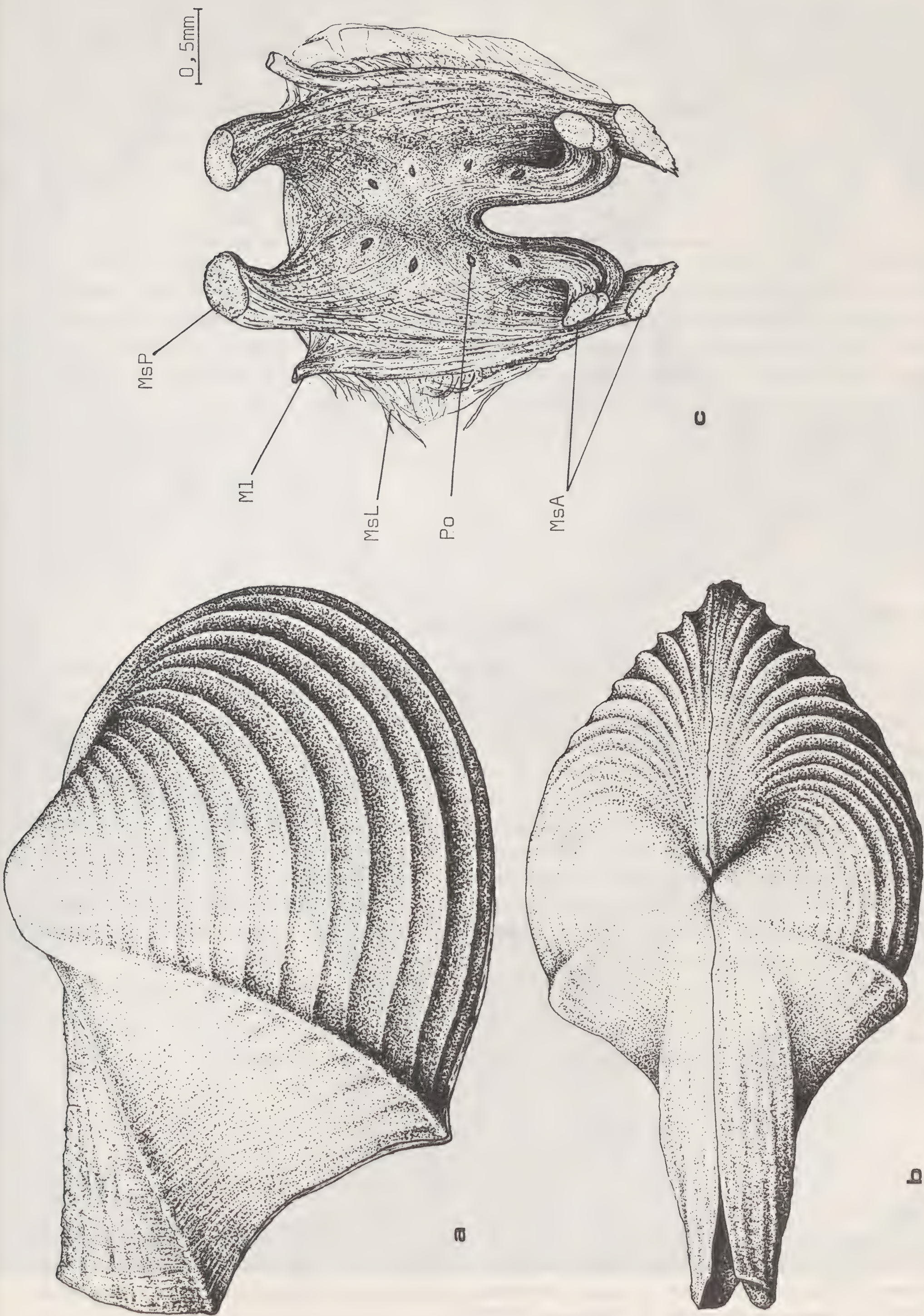


Fig. 5. *Myonera angularis quadrostrata* n.ssp. Benthedi St.87: a-b, vues externes du test, côté droit et vue dorsale; c, septum, vue dorsale (a-b, holotype; c, paratype).



épaissi et finement papilleux à son extrémité postérieure qui est prolongée le long de chaque valve par un revêtement périostracal plissé longitudinalement. Siphon exhalant beaucoup plus petit et plus court que l'inhalant qui occupe la majeure partie du manchon siphonal. Siphons entourés par sept tentacules filiformes, quatre ventralement et trois dorsalement. Ouverture inhalante débouchant dans la chambre infraseptale par l'intermédiaire d'une mince valvule munie en son milieu d'une fente verticale. Pied étroit et cylindrique, à base renflée postérieurement, possédant une longue fente byssale sur sa face postérieure (un filament de byssus sortant d'une petite ouverture située à la base du sillon byssal a été observé sur deux spécimens). Palpes labiaux très petits, s'insérant sur un bourrelet annulaire qui limite extérieurement l'entonnoir buccal: palpes antérieurs formant deux petites expansions digitiformes assez écartées l'une de l'autre et de l'ouverture buccale; palpes postérieurs réduits à de simples protubérances juxtaposées (type I de Allen & Morgan 1981). Septum épais, bosselé et fortement strié, percé de quatre paires de pores. Muscles septaux antérieurs bifides, les plus internes comprenant chacun deux faisceaux de fibres coalescentes à leur point d'insertion sur la coquille; muscles septaux postérieurs épais et non divisés mais bordés extérieurement par un étroit faisceau de fibres longitudinales qui s'insèrent latéralement et postérieurement sur le test. Il existe aussi de chaque côté du septum quelques fibres musculaires transversales convergentes dorsalement.

### Remarques

Les échantillons de Benthedi présentent une nette affinité avec *Myonera angularis* (Jeffreys 1876), en particulier par la disposition des deux côtes radiales de la moitié postérieure du test. Ils s'en distinguent cependant par une extrémité postérieure tronquée et non arrondie, une sculpture rostrale rayonnante bien marquée (côte umbono-postérieure toujours bien développée, rostre nettement ridé longitudinalement), un bord dorsal antérieur haut et régulièrement arrondi au lieu d'être déclive et brusquement arqué en avant, ainsi que des crochets moins proéminents. Par la conformation de la partie postérieure du test, ils se reconnaissent facilement des autres espèces de *Myonera* à côtes, en particulier de *M. dispar* Dall, Bartsch & Rehder 1938 du Pacifique central, de *M. bicarinata* Smith 1896 de l'océan Indien, et de *M. paucistriata* Dall 1886 de l'Atlantique occidental, qui possèdent chacune deux côtes radiales umbono-ventrales (d'après Allen & Morgan 1981, ces trois espèces devraient être considérées comme synonymes).

Bien que les divergences notées plus haut ne rentrent pas dans la variabilité des caractères du test de l'espèce de Jeffreys, il a semblé préférable de considérer le présent matériel comme simple sous-espèce de *M. angularis*, eu égard à la fréquence des espèces dotées d'une vaste aire de distribution chez les Cuspidariidae abyssales.

### Distribution

*Myonera angularis quadrostrata* a été récoltée vivante au sud-est des îles Glorieuses par environ 3700 m de fond. La sous-espèce nominale a été citée de l'Atlantique nord, entre 1818 et 3265 m, ainsi que du golfe du Mexique (530 m!).



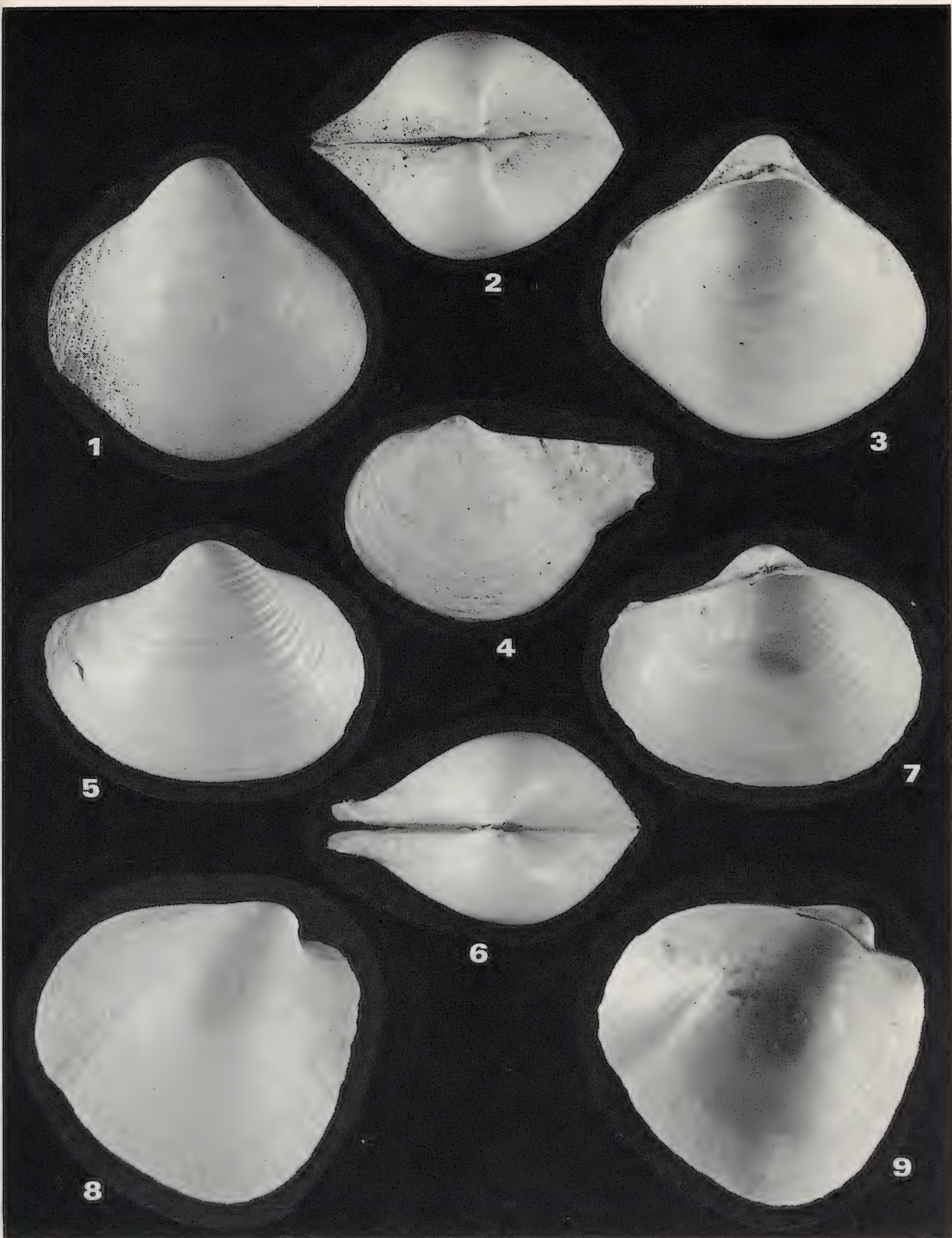


PLANCHE 17

Figs. 1-3, *Poromya tornata* (Jeffreys). Benthedi St.82; 14,8 mm: valve droite, vue externe; vue dorsale; valve gauche, vue interne.

Fig. 4, *Cuspidaria barnardi* Knudsen. Benthedi St.87; 12 mm: valve gauche, vue externe.

Figs. 5-7, *Cuspidaria undata* (Verrill). Safari St.11 CP 06; 21 mm: valve droite, vue externe; vue dorsale; valve gauche, vue interne.

Figs. 8-9, *Lyonsiella galathea* (Knudsen). Benthedi St.87; 7,2 mm: valve droite, vue externe; valve gauche, vue interne.







**Protocuspidaria (Edentaria) thomassini** n.sp. (Fig. 6a–b)*Matériel*

Benthedi St.87, 3.04.77, sud-est des Glorieuses, 11°44'S, 47°35'E, 3716 m: 1 exemplaire vivant (holotype).

Holotype: MNHN.

*Description*

Largeur 3,8 mm, hauteur 3,1 mm, renflement 1,7 mm (holotype). Coquille modérément renflée, équivalve, inéquilatérale, un peu plus large que haute, de contour ovalaire et rostré postérieurement, à test blanchâtre et baïllant en arrière. Crochets peu saillants, situés au tiers antérieure de la largeur des valves. Bord dorsal antérieur convexe, assez court, se raccordant sub-anguleusement avec le bord antérieur qui est haut et quelque peu aplati. Bord ventral régulièrement arrondi, faiblement sinué au contact du rostre. Rostre court et tronqué en arrière, relativement haut, relié au reste du test par une faible dépression rayonnant de l'arrière des crochets à la sinuosité postéro-ventrale des valves. Bord dorsal postérieur assez long, subrectiligne, non déclive. Sculpture externe d'aspect finement rugueux et irrégulier, composée essentiellement de petites stries et rides concentriques plus ou moins anastomosées. Sculpture du rostre plus saillante, formant des plis concentriques irréguliers, et comportant un ou deux cordonnets rayonnants qui s'atténuent rapidement en arrière. Au niveau de la dépression umbono-postérieure, on peut observer des stries légèrement obliques recoupant à la fois la sculpture concentrique du rostre et celle du disque, ce qui rend cette région du test confusément treillissée. Sculpture externe des valves disparaissant au voisinage de la marge dorsale antérieure, ce qui tend à former une sorte de lunule. Périostracum adhérent, beige, translucide, devenant plus sombre et fibreux à la périphérie des valves où il rehausse la sculpture externe (notamment au niveau du rostre), débordant largement sur la face interne du test.

Ligament interne beige-corné, grossièrement trigone, incliné vers l'arrière, indentant la marge cardinale au-dessous et en arrière des crochets.

Charnière complètement dépourvue de dents, mince en arrière du résilium. Surface

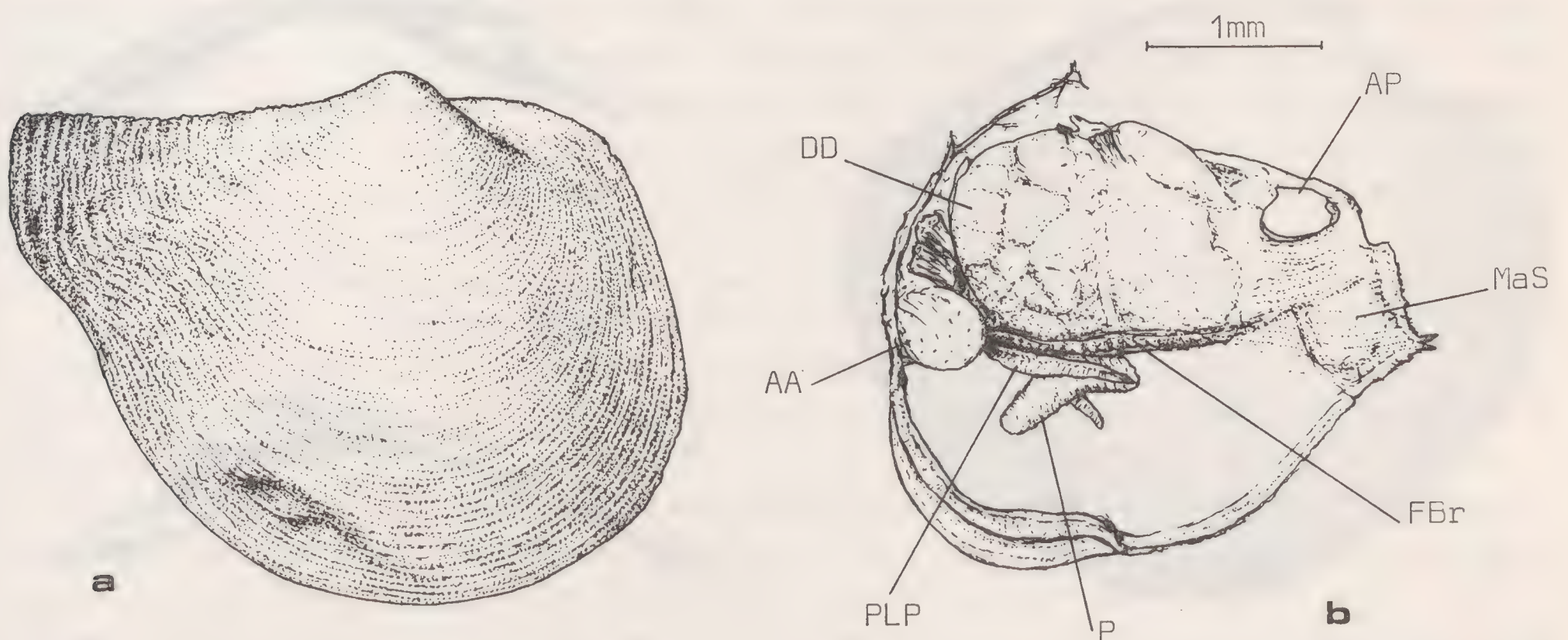


Fig. 6. *Protocuspidaria thomassini* n.sp. Holotype: a, valve droite, vue externe; b, parties molles, vues du côté gauche.



interne du test luisante, d'un blanc laiteux, pratiquement lisse. Empreintes musculaires indistinctes. Marges internes lisses.

Parties molles: Manteau assez mince, à ouverture pédieuse s'étendant environ sur le tiers antérieur de la marge palléale qui n'est que modérément épaisse. Manchon siphonal mince, délicatement frangé à son extrémité postérieure qui est aussi finement ridée et épaissie intérieurement. Siphon exhalant plus petit et plus court que le siphon inhalant. Sept tentacules de forme simple, légèrement claviforme (type 'club' de Allen & Morgan 1981) entourent les siphons, quatre au niveau du siphon inhalant et trois au niveau de l'exhalant. Pied trapu et conique, fortement ridé transversalement (ce qui correspond peut-être à un phénomène de rétraction), avec une fente byssale sur la face postérieure et une forte protubérance basale en arrière. Palpes labiaux très dissymétriques, les antérieurs réduits à de minces languettes trigones, les postérieurs longs et étroits, pliés en deux longitudinalement, s'étendant vers l'arrière jusqu'à la protubérance basale postérieure du pied. Septum mince, muni de deux séries de fentes branchiales bien développées; ces dernières s'étendant de part et d'autre du pied jusqu'à l'extrémité postérieure du septum et comptant chacune une trentaine de fentes. Muscles adducteurs des valves ovalaires, de taille peu inégale, le postérieur toutefois un peu plus petit.

### Remarques

Par l'aspect général de son test et par la conformation de ses parties molles (notamment par la présence de structures branchiales nettes et par les caractères de la région siphonale), cette espèce correspond au genre *Protocuspидaria* Allen & Morgan 1981. Sa charnière complètement édentule la rapproche de *Protocuspидaria* (*Edentaria*) *simplis* Allen & Morgan 1981 de l'Atlantique septentrional et central; cependant, elle s'en écarte nettement par son rostre plus gracile et plus long ainsi que par l'aplatissement de son bord antérieur. Par rapport à *Myonera ruginosa* (Jeffreys 1881), espèce à charnière édentule de l'Atlantique occidental dont Verrill & Bush (1898, p. 811, pl. 72 Fig. 4, pl. 74 Fig. 2) ont donné une description précise du test (mais dont on ne connaît malheureusement pas les parties molles), *Protocuspидaria thomassini* se distingue par ses crochets antérieurs et non sub-médians, par sa

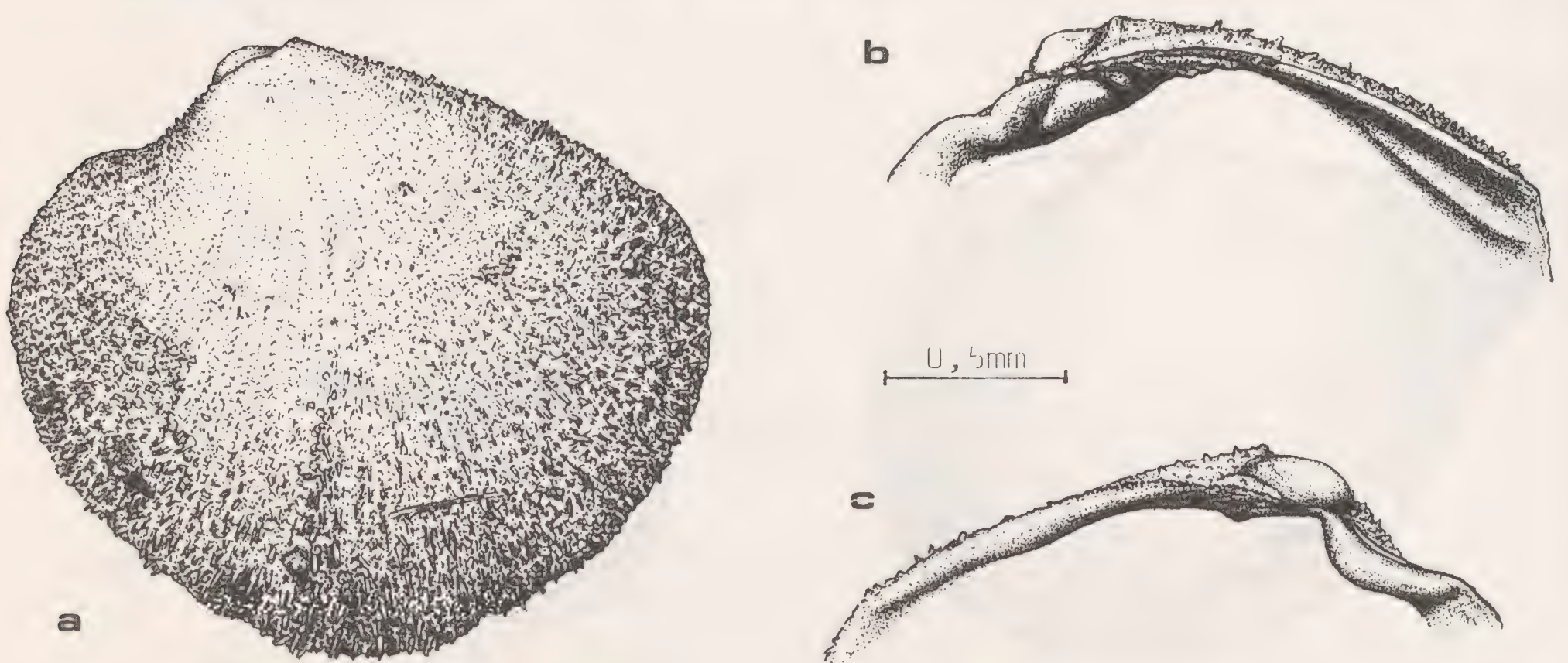


Fig. 7. *Verticordia excoriata* n.sp. Holotype: a, valve gauche, vue externe, 1,8 mm; b, charnière de la valve droite, vue interne; c, charnière de la valve gauche, vue interne.



moitié antérieure dont le contour est aplati en avant et subanguleux dorsalement au lieu de semi-circulaire, et par son résilium moins obliquement penché vers l'arrière.

### *Distribution*

Cette espèce n'est connue que par le type et unique spécimen, récolté vivant au sud-est des îles Glorieuses par 3716 m de fond. Elle est la première du genre *Protocrepidaria* à être trouvée en dehors de l'océan Atlantique.

VERTICORDIIDAE Stoliczka 1871

### **Verticordia excoriata** n.sp. (Fig. 7a–c)

#### *Matériel*

Benthedi St.90, 4.04.77, sud-est des Glorieuses, 11°44'S, 47°30'E, 3700 m: 1 valve droite (paratype) et 1 exemplaire vivant (holotype).

Holotype: MNHN.

#### *Description*

Largeur 1,8 mm, hauteur 1,5 mm, renflement 1,3 mm (holotype). Coquille subéquivalve, modérément renflée, inéquilatérale, un peu plus large que haute, de contour ovale subtrigone, à test blanchâtre et assez épais. Crochets peu saillants, situés vers le tiers antérieur des valves, dirigés vers l'intérieur et vers l'avant. Bord dorsal antérieur assez court, s'inclinant fortement vers le bas antérieurement. Bord antérieur régulièrement arrondi, se raccordant sans discontinuité avec le bord ventral qui devient un peu plus convexe au niveau de la ligne médiane du test. Bord postérieur largement arqué, tendant à former une angulosité mousse avec le bord dorsal postérieur qui est long, un peu déclive et légèrement convexe. Surface externe des valves convexe, excoriée dans la région umbonale, avec une petite lunule renfoncée en avant des crochets et une faible ride rayonnante qui longe le bord dorsal postérieur. Valve droite tendant à déborder extérieurement sur l'autre valve, très faiblement au niveau du bord dorsal postérieur, mais plus nettement au niveau de la lunule, ce qui rend le test un peu inéquivalve. Sculpture externe composée uniquement de très nombreuses épines microscopiques disposées suivant des lignes radiales irrégulières et serrées qui tendent à retenir des particules de substrat. Périostracum mince, adhérent, translucide, débordant sur la marge interne du test où il apparaît déjà garni d'épines.

Ligament externe formant en arrière des crochets une petite bande brune contre le bord dorsal postérieur des valves. Ligament interne renforcé par un lithodesme et formant dans chaque valve une empreinte longue et mince qui s'étend obliquement vers l'arrière depuis la cavité umbonale.

Charnière de la valve droite avec une dent cardinale épaisse, en forme de tubercule arrondi; à l'intérieur de la valve droite, dans la moitié terminale du bord dorsal postérieur, se trouve un long sillon limité par une ride latérale interne légèrement divergente vers l'arrière. Charnière de la valve gauche avec un faible épaissement latéral postérieur, et une dent latérale antérieure qui vient s'insérer sous l'expansion lunulaire de l'autre valve. Surface



interne du test d'un blanc luisant. Empreintes musculaires peu nettes à l'exception de celle de l'adducteur antérieur qui est fortement marquée. Empreinte adductrice postérieure plus grande que l'antérieure. Ligne palléale assez large et non sinuée. Marges internes lisses.

### Remarques

L'holotype de *Verticordia excoriata* ayant été conservé à sec, il n'a pas été possible d'en observer correctement les parties molles, ni de vérifier s'il correspondait bien à un exemplaire sexuellement mature. Le lithodesme, fragmenté, n'a pu être reconstitué. Le test de la valve droite dépareillée ne présente pas de différences notables avec celui de l'holotype, si ce n'est une taille supérieure (3,0 mm de large) et un contour légèrement plus arqué en arrière.

*V. excoriata* fait partie d'un groupe d'espèces sans côtes radiales saillantes et de taille souvent modeste, identifié par certains auteurs au genre *Vertambitus* Iredale 1930. *Verticordia affinis* Thiele & Jaeckel 1931 de l'océan Indien occidental, se distingue de cette nouvelle espèce par son contour rhomboidal, plus anguleux ventralement, ainsi que par l'absence de dent latérale à la valve gauche. *V. quadrata* Smith 1885 de l'Atlantique tropical, en diffère par ses crochets plus saillants, son bord ventral moins régulièrement arrondi et les épines de la surface externe ne formant pas de rangées radiales. Enfin, *V. woodi* Smith 1885 de l'Atlantique tropical, se reconnaît à sa forme plus étirée en hauteur ainsi qu'au détail de la conformation de sa charnière (pas de dent latérale antérieure mais présence d'un dentelon cardinal à la valve gauche, pas de ride postérieure interne à la valve droite).

### Distribution

*Verticordia excoriata* n'est connue que de la localité type située au sud-est des îles Glorieuses, par 3700 m de fond.

### **Lyonsiella curta** n.sp. (Fig. 8a–e)

#### Matériel

Benthedi St.87, 3.04.77, sud-est des Glorieuses, 11°44'S, 47°35'E, 3716 m: 1 exemplaire vivant (holotype).

Benthedi St.90, 4.04.77, sud-est des Glorieuses, 11°44'S, 47°30'E, 3700 m: 5 exemplaires vivants (paratypes).

Holotype: MNHN.

#### Description

Largeur 6,3 mm, hauteur 5,7 mm, renflement 4,8 mm (holotype). Coquille inéquivalve, renflée, un peu plus large que haute, inéquilatérale, de contour subtrapézoïdal, à test blanchâtre et opaque; ligne de commissure des valves rendue un peu sinueuse par la marge de la valve droite qui déborde dorsalement et ventralement sur l'autre valve. Crochets renflés et saillants, situés très en avant du test, fortement recourbés vers l'intérieur et vers l'avant. Bord dorsal antérieur très court, déclive. Bord antérieur arrondi, se raccordant sans discontinuité avec le bord ventral qui est faiblement arqué. Bord postérieur haut et



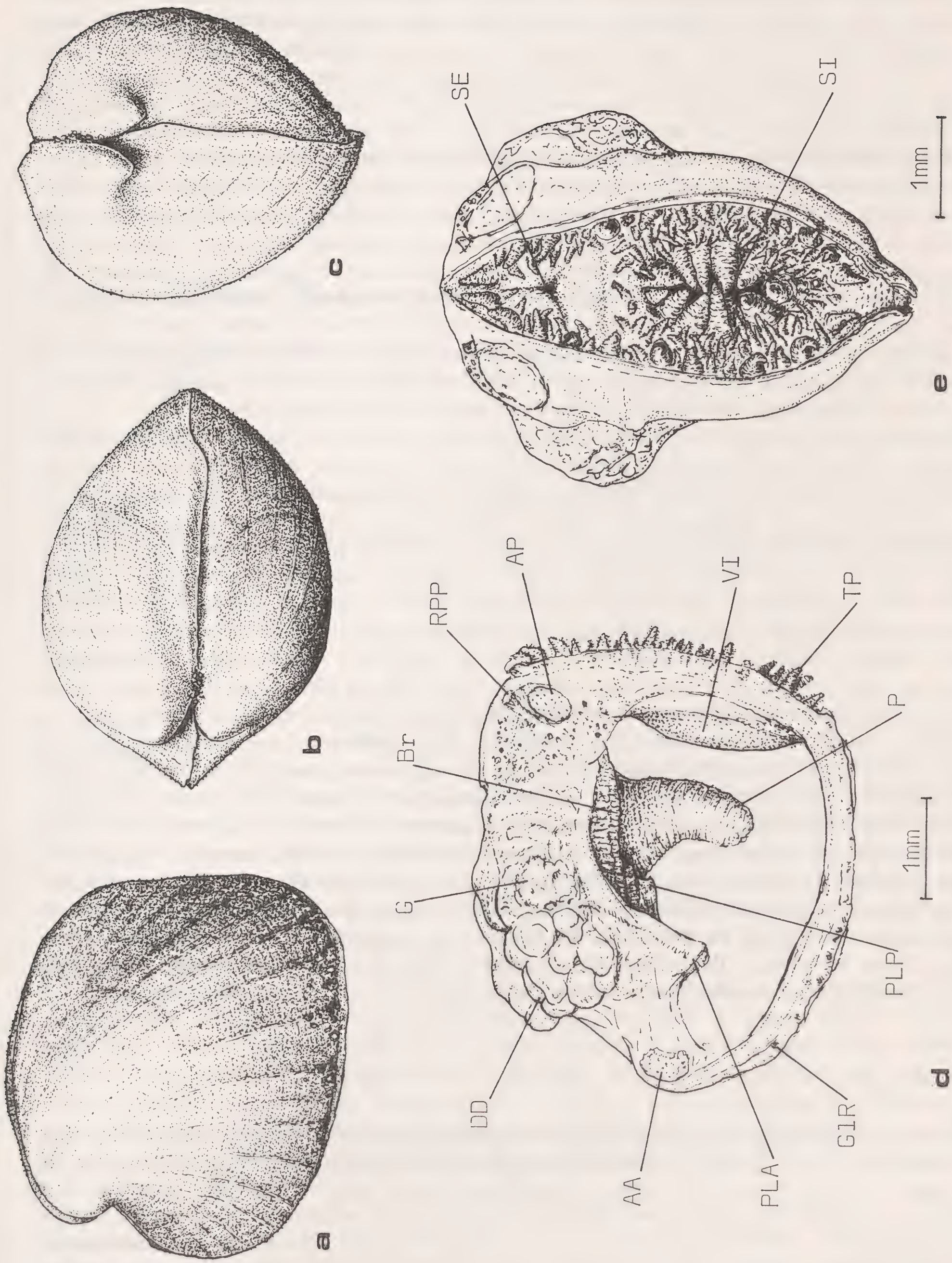


Fig. 8. *Lyonsiella curta* n.sp.: a-c, vues externes du test, côté gauche, vues dorsale et antérieure; d-e, parties molles, vue du côté gauche et vue postérieure (a-c, holotype, 6,3 mm; d-e, paratypes, Benthedi St.90).



subrectiligne, tendant à former avec le bord ventral et avec le bord dorsal postérieur une angulosité émoussée. Bord dorsal postérieur largement arqué au-dessus de l'horizontale. Surface externe des valves bien convexe, avec un renflement maximum selon une zone rayonnant des crochets à l'extrémité postéro-ventrale du test. Une dépression radiale large mais peu profonde s'étend de l'arrière des crochets au tiers supérieur du bord postérieur du test qu'elle tend à rendre un peu sinueux. Marge dorsale postérieure rebordée par une ride radiale un peu plus saillante à la valve droite qu'à la gauche. Zone dorsale de chaque valve un peu déprimée en avant des crochets, formant une sorte de lunule mal délimitée mais nettement plus développée à la valve droite qui déborde extérieurement sur l'autre valve. Sculpture externe de chaque valve comprenant environ vingt lignes rayonnantes croisées par de fines marques concentriques d'accroissement; toute la surface externe apparaît de plus couverte de très nombreuses et petites granulations plus ou moins alignées en rayons serrés. Périostracum gris-beige, mince et adhérent, un peu épaissi sur les lignes rayonnantes et à la périphérie des valves où il tend à retenir des particules de substrat, débordant sur la face interne des valves.

Ligament externe brunâtre, bien développé, formant une mince bande arquée qui s'étend en arrière des crochets sur la majeure partie du bord dorsal postérieur. Ligament interne assez court, renforcé par un lithodesme étroit et de contour rectangulaire.

Charnière très mince et complètement dépourvue de dents. Surface interne du test blanchâtre et luisante. Empreintes musculaires assez peu nettes, à l'exception de celle de l'adducteur antérieur qui est ovale subquadratique. Empreinte adductrice postérieure effilée en pointe dorsalement. Ligne palléale large et dépourvue de sinus. Marges internes lisses.

Parties molles: Ouverture pédieuse du manteau s'étendant sur la moitié antérieure de la marge ventrale qui est munie de petites glandes palléales radiales. Ouverture du siphon inhalant large, entourée de six paires de tentacules forts et coniques, couverts de villosités microscopiques. Siphon inhalant prolongé intérieurement par une valvule robuste mais très courte. Siphon exhalant peu saillant, formant un bourrelet subcirculaire, à ouverture nettement plus réduite que l'ouverture inhalante dont elle est séparée par un espace assez vaste. Autour des deux siphons s'étend une zone plane, un peu épaissie par rapport au manteau et garnie de tentacules. Tentacules de la périphérie alternativement petits et grands, mais moins bien développés que ceux du siphon inhalant. Entre les tentacules périphériques et les siphons, on peut encore distinguer de nombreux petits tentacules disposés irrégulièrement; ils se répartissent approximativement en deux rangs concentriques autour du siphon inhalant, mais en un seul rang dorsalement et latéralement par rapport au siphon exhalant. Pied bien développé, allongé, avec une fente byssale sur la face postérieure. Palpes labiaux soudés, constituant une sorte d'entonnoir buccal: les antérieurs soudés latéralement aux parois du manteau, les postérieurs tendant à former deux languettes trigones libres en arrière. Branchies non attachées au pied, libres vers l'arrière sauf à leur extrémité postérieure où elles sont soudées entre elles.

### Remarques

Par son aspect général, la coquille de *Lyonsiella curta* rappelle celle de *L. quaylei* Bernard (1969, p. 2232, Fig. 3; 1974, p. 112, pl. 29 Figs. 2-3) du Pacifique oriental. Cependant, elle s'en écarte par une forme plus courte, proportionnellement plus haute et tronquée en arrière. Par rapport à *L. perplexa* Allen & Turner 1974 de l'Atlantique du nord-est, cette nouvelle espèce se distingue par la présence de lignes radiales à la surface des valves, par son bord dorsal arqué et non subrectiligne, ainsi que par des particularités de l'anatomie de ses parties molles (ouverture pédieuse du manteau ne s'étendant pas sur toute la longueur de la marge ventrale qui possède des glandes radiales, présence de nombreux tentacules en plus des six paires qui



bordent le siphon inhalant). Enfin, *L. curta* se reconnaît de *L. parva* Okutani (1962, p. 29, pl. 3 Fig. 7; 1968, p. 17, pl. 2 Fig. 2) du Pacifique occidental, par sa forme encore plus trapue ( $h/l=0,86$  chez *L. parva*, 0,89 à 0,96 chez *L. curta*), son bord dorsal postérieur non dilaté en arrière et formant un angle plus ouvert avec le bord postérieur.

#### *Distribution*

*L. curta* a été récoltée vivante vers 3700 m de profondeur, au sud-est des îles Glorieuses.

**Lyonsiella galathea** (Knudsen 1970). (pl. 17, Figs. 8–9)

*Laevicordia galathea* Knudsen 1970, p. 128, Figs. 85–86.

*Lyonsiella galathea* Allen & Turner 1974, p. 525.

#### *Matériel*

Benthedi St.87, 3.04.77, sud-est des Glorieuses, 11°44'S, 47°35'E, 3716 m: 6 exemplaires vivants.

Benthedi St.90, 4.04.77, sud-est des Glorieuses, 11°44'S, 47°30'E, 3700 m: 12 exemplaires vivants.

#### *Remarques*

L'examen du présent matériel a fait apparaître certaines différences par rapport à la définition originale de *L. galathea*, à laquelle il correspond par ailleurs assez bien. Toutefois, il semble que ces divergences soient surtout le fait d'une variabilité des caractères, peut-être en rapport avec des phénomènes d'ontogénie. C'est ainsi que le test, qui est nacré et plus ou moins translucide, peut avoir un contour variablement étiré en arrière et présenter une légère dépression rayonnant des crochets au tiers supérieur du bord postérieur. En ce qui concerne les parties molles on a compté jusqu'à 14–15 paires de tentacules autour du siphon inhalant, au lieu de 20 paires environ chez le type de Knudsen; cependant, les exemplaires de Benthedi sont tous nettement plus petits que ceux de Knudsen (7,8 mm au maximum au lieu de 17 et 14,8 mm respectivement pour les type et paratype).

D'un point de vue systématique, il apparaît un certain désaccord entre les auteurs modernes dans l'acception du genre *Laevicordia* Seguenza 1876. Knudsen (op.cit.) reprend la conception de Soot-Ryen (1966, p. 24) selon laquelle ce genre comprend les espèces de contour 'suborbiculaire' rapelant le genre *Policordia*, mais pourvues d'une fine granulation externe comme chez *Lyonsiella*. Allen & Turner (1974, p. 408) restreignent la définition de ce genre aux formes pourvues d'une granulation externe, mais ne présentant pas de stries ou rides rayonnantes (ce qui en élimine la plupart des espèces répertoriées jusqu'alors).

#### *Distribution*

Cette espèce n'était connue à ce jour que par le matériel type de Knudsen, dragué au large du sud-Kenya par 4820 m de profondeur.



**Lyonsiella cf. formosa** (Jeffreys 1881). (Fig. 9)

*Lyonsia formosa* Jeffreys 1881, p. 930, pl. 70 Fig. 1-1a; Barnard 1964, p. 571; Nordsieck 1969, p. 157, pl. 22 Fig. 90.03.

*Lyonsiella formosa* Allen & Turner 1974, p. 447, Figs. 43-49, appendice p. 524.

*Matériel*

Benthedi St.87, 3.04.77, sud-est des Glorieuses, 11°44'S, 47°35'E, 3716 m: 1 exemplaire vivant.

*Remarques*

L'exemplaire de la st.87 répond bien aux descriptions et illustrations que Allen & Turner (1974) ont données de l'espèce de Jeffreys. Toutefois, on a pu noter quelques différences dans les parties molles du présent spécimen (l'ouverture pédieuse est limitée aux deux tiers antérieurs de la marge palléale, les tentacules périssiphonaux sont plus nombreux). L'exemplaire de Benthedi ne possède pas, malgré sa taille relativement grande (8,8 mm de longueur), de rides obliques flexueuses dans la région antérieure du test. Ceci semble le rapprocher des échantillons de Allen & Turner (qui ne mentionnent ni ne figurent cette sculpture très particulière), mais l'écarte de spécimens classiquement attribués à l'espèce de Jeffreys par divers auteurs (cf. en particulier Smith 1885, pl. 6 Fig. 3-3b; Locard 1898, p. 218; Sturany 1896, p. 15, pl. 1 Figs. 14-16). Cette sculpture semble apparaître assez rapidement au cours de l'ontogénie, ainsi qu'on a pu le vérifier sur des échantillons bathyaux de la collection Locard. Ceci pose un problème quant à la variabilité éventuelle du test chez *L. formosa*, et suggère même la présence de deux formes spécifiquement distinctes dans le domaine atlantique, l'une bathyale et l'autre abyssale.

En ce qui concerne cette espèce, il faut encore signaler les importants problèmes que soulève son attribution générique. Placée initialement par son créateur dans la famille des Lyonsiidae, *Lyonsia formosa* a été transférée à la famille des Verticordiidae par Allen &



Fig. 9. *Lyonsiella cf. formosa* (Jeffreys). Benthedi St.87: valve gauche, vue externe, 8,8 mm.



Turner. Ce point de vue est soutenu par le fait qu'on considère souvent les Verticordiidae (et notamment les formes du genre *Lyonsiella* chez lesquelles la réduction branchiale est encore limitée) comme dérivant d'Anomalodesmata du type *Lyonsia*. Cependant, W. H. Dall avait fait de *L. formosa* le type de *Allogramma*, taxon considéré d'abord comme section de *Entodesma* Philippi (Dall 1903, p. 1514), puis comme sous-genre de *Lyonsia* Turton (Dall, Bartsch & Rehder 1938, p. 215), ou même comme genre (Habe 1977, p. 305). Plusieurs espèces de l'Indo-Pacifique ont été attribuées à *Allogramma* Dall, et semblent morphologiquement assez proches de l'espèce type. De plus, R. Prezant (1981), qui vient de tenter une redéfinition des coupures d'ordre générique chez les Lyonsiidae, en conclut que *Allogramma* doit être considérée comme simple synonyme de *Lyonsia*, ce qui apparaît en contradiction avec l'opinion de Allen & Turner (à laquelle il ne fait malheureusement pas allusion). Il semble donc à l'heure actuelle important de reconsidérer la position systématique de *Allogramma* ainsi que sa composition spécifique; l'étude détaillée des espèces de ce taxon pourrait en effet apporter des éclaircissements sur les liens de parenté entre Verticordiidae et Lyonsiidae et leurs délimitations respectives.

Ne pouvant résoudre, dans le cadre restreint de cet article, les divers problèmes abordés dans ces remarques, on n'a attribué qu'avec réserves l'exemplaire de Benthedi à *Lyonsiella formosa* (sensu Allen & Turner 1974).

### Distribution

*L. formosa* (s.l.) a été citée de Méditerranée (Sturany, op.cit.; Mars 1965), des golfes de Gascogne et du Mexique, des îles Canaries et des Açores, de l'Atlantique équatorial (Allen & Turner 1974) et du large de l'Afrique du Sud (Barnard 1964), entre 366 et 3783 m de profondeur.

### REMARQUES GENERALES

Les recherches récentes (Odhner 1960, Knudsen 1967, 1970, Ivanova 1977, Allen et. al. 1974, 1981) ont montré l'importance des parties molles dans la définition des taxons chez les Septibranches. Ainsi, chez les Poromyidae, les genres *Cetoconcha* et *Poromya* peuvent se distinguer aisément par la conformation de leurs oscules septaux; chez les Cuspidariidae, le genre *Protocuspidaria* se caractérise par la présence de nombreuses fentes branchiales; chez les Verticordiidae, le nombre, l'aspect et la disposition des tentacules péricéphaux peuvent fournir des critères d'identification pour différentes espèces du genre *Lyonsiella* (sensu Allen & Turner 1974). Cependant, la délimitation de nombreux taxons, l'origine et l'homogénéité du groupe des Septibranches étant aujourd'hui encore matière à controverses chez les différents auteurs (Bernard 1979, Scarlato & Starobogatov 1979, Scarlato 1981, Morton 1981), il a paru raisonnable, dans le cadre restreint de cet article, d'utiliser une classification proche de celle de Newell (in R. C. Moore 1969, pp. 205–224) et Keen (ibid., pp. 852–857).

Les Septibranches récoltés lors de la campagne Benthedi proviennent d'un ensemble d'environ 30 espèces de Bivalves abyssaux; ils représentent donc quelques 40% du total des espèces rencontrées. Parmi ces Bivalves abyssaux de Benthedi, seul le groupe des Paléotaxodontes représente un autre ensemble important, tant du point de vue du nombre des spécimens récoltés que de la diversité spécifique. Ceci s'accorde avec les observations de Knudsen (1970, pp. 180–187), bien que les Septibranches apparaissent ici comme les plus diversifiés. D'autre part, le nombre important de formes nouvelles montre, une fois encore, l'imperfection des connaissances sur la faune malacologique profonde.



Parmi les espèces récoltées, certaines ont une vaste répartition géographique s'étendant à l'océan Atlantique (*Poromya tornata*, *Cetoconcha transversa*, *Cuspidaria barnardi*, *Cuspidaria undata*, *Myonera angularis*, et peut-être *Lyonsiella formosa*). D'autres espèces n'ont été trouvées que dans l'océan Indien (*Lyonsiella galathea* et les quatre espèces nouvelles de ce travail). Enfin, aucune espèce du Pacifique n'a été rencontrée ici.

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# *FUSINUS (SINISTRALIA) SOMALIENSIS*: A NEW SPECIES OF WHELK FROM MOGADISCIO, SOMALIA

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(Accepted for publication, 15 December 1983)

*Abstract:* *Fusinus (Sinistralia) somaliensis* is described as a new species from Mogadiscio, Somalia. Other species of this sinistral subgenus are discussed and the holotypes of *F. (S) elegans*, *F. (S) barclayi* and '*Fusus*' *taylorianus* are figured. A lectotype of *Fusinus taylorianus* (Reeve) is designated.

## INTRODUCTION

Whilst investigating the identity of a species of sinistral whelk from Oman (*Fusinus (Sinistralia) gallagheri* Smythe & Chatfield 1981) one of the authors (JEC) came across two shells of an un-named specimen of this subgenus in the collections of the Academy of Natural Sciences, Philadelphia, U.S.A. This was not the same as the species from Oman and no further work was done on them apart from notes and photographs taken at the time in Philadelphia. Subsequently the other author (KRS) was in correspondence with Dr Harry G. Lee of Florida who wrote to her enquiring about the identity of specimens of *Fusinus (Sinistralia)* from Somalia in his possession. These he kindly loaned for study when it became apparent that they were the same as the unidentified species in the Academy of Natural Sciences, Philadelphia, and also shells which Dr Lee had seen in the American Museum of Natural History, New York. These un-named specimens we now describe as *F. (S) somaliensis* sp. nov. In addition to this description we also summarise the known species in this little studied subgenus of left-handed whelks.

## FUSINUS (SINISTRALIA) SOMALIENSIS SP. NOV.

Shell moderately solid, sinistral, with the spire about one half of the total height. Shell height (holotype) 25.5 mm, breadth 12.6 mm, whorls 5 plus protoconch. Sutures distinct, siphonal canal comparatively long (4 mm) and only slightly directed at an angle away from the aperture. There are no columellar folds. Mouth (aperture) pear-shaped; inner lip with the peristome having linear teeth which are inward projections of the grooves between the spiral ridges of the outside of the shell; these do not project far into the mouth. At the top of the aperture is a small notch and tooth that also occur in other species of *Sinistralia*. Shell sculpture is dominated by strong spiral ridges (14 on the body whorl of the holotype), broad ones alternating with narrow ones. The whorls are crossed by distinct longitudinal costae (9 on the body whorl). The shell is a uniform cinnamon brown but often obscured by lime

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encrustation on the spire. Protoconch smooth and colourless, followed by a brown teleoconch with the beginning of axial ribbing.

Type locality: Mogadiscio, Somalia.

Holotype: American Museum of Natural History, New York. Registered number 120348. Collected by Mrs Orville Davis, 1963–1964 (Plate 18a).

Paratypes:

- 1 American Museum of Natural History, 3 paratypes, data as for holotype (Plate 18d).
- 2 Academy of Natural Sciences, Philadelphia, U.S.A. Registered number ANSP 289962. Two specimens found on a reef 14 km north of Mogadiscio by Adelaide C. Davis, 31 October 1962.
- 3 British Museum (Natural History), London, U.K. Registered number 1983061 One specimen from Mogadiscio, ex Harry G. Lee Collection (details below).
- 4 The collection of Dr Harry G. Lee of Jacksonville, Florida, U.S.A. Three specimens obtained from local shell vendors of Mogadiscio, 1973–1980 (Plate 18b-c).

#### OTHER SPECIES OF *SINISTRALIA*

H. and A. Adams erected the sub-genus *Sinistralia* in 1853 (Saunders 1978) to include *Murex maroccanus* Chemnitz, *Buccinum scaevolum* Meunsch and *Fusus elegans* Reeve 1848. Gmelin re-described the first species as *Murex maroccensis* in 1791 and this is the type species of the subgenus. It appears to be distributed along the north-western coast of Africa and into the Atlantic. It may well be a composite of several species or subspecies and is currently being studied in greater detail by Dr Harry G. Lee.

*Buccinum scaevolum* Meunsch 1787 is probably *Fusinus (Sinistralia) maroccensis*, if identifiable at all. (Dr Lee, pers. commun.).

'*Fusus*' *taylorianus* Reeve 1848 (Plate 19a–b) was described and the dextral shell figured in *Conchologia Iconica* 2, plate 20, Fig. 85. The two syntypes, one dextral and the other sinistral, are in the British Museum (Natural History) and are clearly different species. The sculpture is different, the siphonal canal of the dextral specimen is longer and the sinistral shell has the notch and tooth at the top of the aperture which are absent in the dextral one. The dextral shell measures 17.8 mm by 8.5 mm and the sinistral one 17.2 mm by 7 mm. It would appear that the sinistral specimen lacks a name as it differs from the figured dextral specimen which we here designate as the lectotype of *Fusinus taylorianus* (Reeve), BM(NH) registered number 1874.12.11.168.

The sinistral species appears to be a *Fusinus (Sinistralia)* species as it has a typical protoconch and has the apertural notch and tooth, but we do not propose to name it as there is only the one unlocalised specimen and this is very worn.

*Fusinus (Sinistralia) elegans* (Reeve 1845) (Plate 19c) was described and figured in *Conchologia Iconica* 2, plate 21, fig. 87 and the holotype is in the British Museum (Natural History). The shell measures 14.2 mm by 4.5 mm; it is very slender, elongate, fusiform, light in weight and pure white in colour. It is spirally ribbed and has longitudinal varices. The area directly below the suture is concave and free from ridges or ribs. In that feature it differs from *F. (S.) maroccensis* which has both elements of sculpture extending to the sutures. The latter is also wider in proportion to its length and is brownish in colour.

'*Fusus*' *depictus* Sowerby 1880. This was described and figured in *Thesaurus Conchyliorum* 5, plate 8, fig. 86. It shows a broadly fusiform shell with peripheral nodules on the shoulders, beige in colour and marked with two bands of chestnut reticulated flammules. The type specimen has not been located and the shell depicted, although sinistral, does not appear to



belong to the genus *Fusinus*, having a wider aperture and a broad, short siphonal canal. There is no information on the habitat or locality and we doubt if it is a marine species.

*Fusinus (Sinistralia) barclayi* (Sowerby 1895). This species was described and illustrated by Sowerby in 1895 and the holotype is in the British Museum (Natural History) (Plate 19d–e). This shell measures 27·2 mm by 14·2 mm and the type locality is Bay of Zaila, Somaliland. There is a specimen from Socotra (collected 1919) in the Muséum National d'Histoire Naturelle, Paris.

*F. (S.) gallagheri* was described and figured by the authors in 1981.

## DISCUSSION

*F. (S.) gallagheri* differs from all the other species in having a much heavier and more solid shell; it and the sinistral syntype of '*Fusus*' *taylorianus* both have rounded, comparatively smooth varices. *F. (S.) somaliensis* resembles the other species of *Sinistralia*, except *F. (S.) gallagheri*, in having a light weight shell, in having the apertural notch and tooth and in the protoconch. In all the known species, the protoconch consists of a smooth apex, followed by an axially ribbed teleoconch (Smythe & Chatfield 1981, pl 17c). *F. (S.) somaliensis* resembles *F. (S.) barclayi* in having a comparatively short spire, about half the total height, and in having a slight peripheral keel, particularly on the body whorl, this is much more exaggerated in *F. (S.) barclayi*. It differs from the latter in colour, the much stronger spiral ribbing and the more posterior position of the peripheral keel. In *F. (S.) maroccensis*, *F. (S.) elegans* and '*F. taylorianus*' the spire height is distinctly more than half the total height and the whorls are rounded rather than angular.

## ACKNOWLEDGEMENTS

For the loan of specimens we are grateful to Dr W. Emerson, American Museum of Natural History; Dr R. Robertson, Academy of Natural Sciences, Philadelphia; Muséum d'Histoire Naturelle, Paris; and Dr Harry G. Lee of Florida. Access to type specimens was made available by the British Museum (Natural History).

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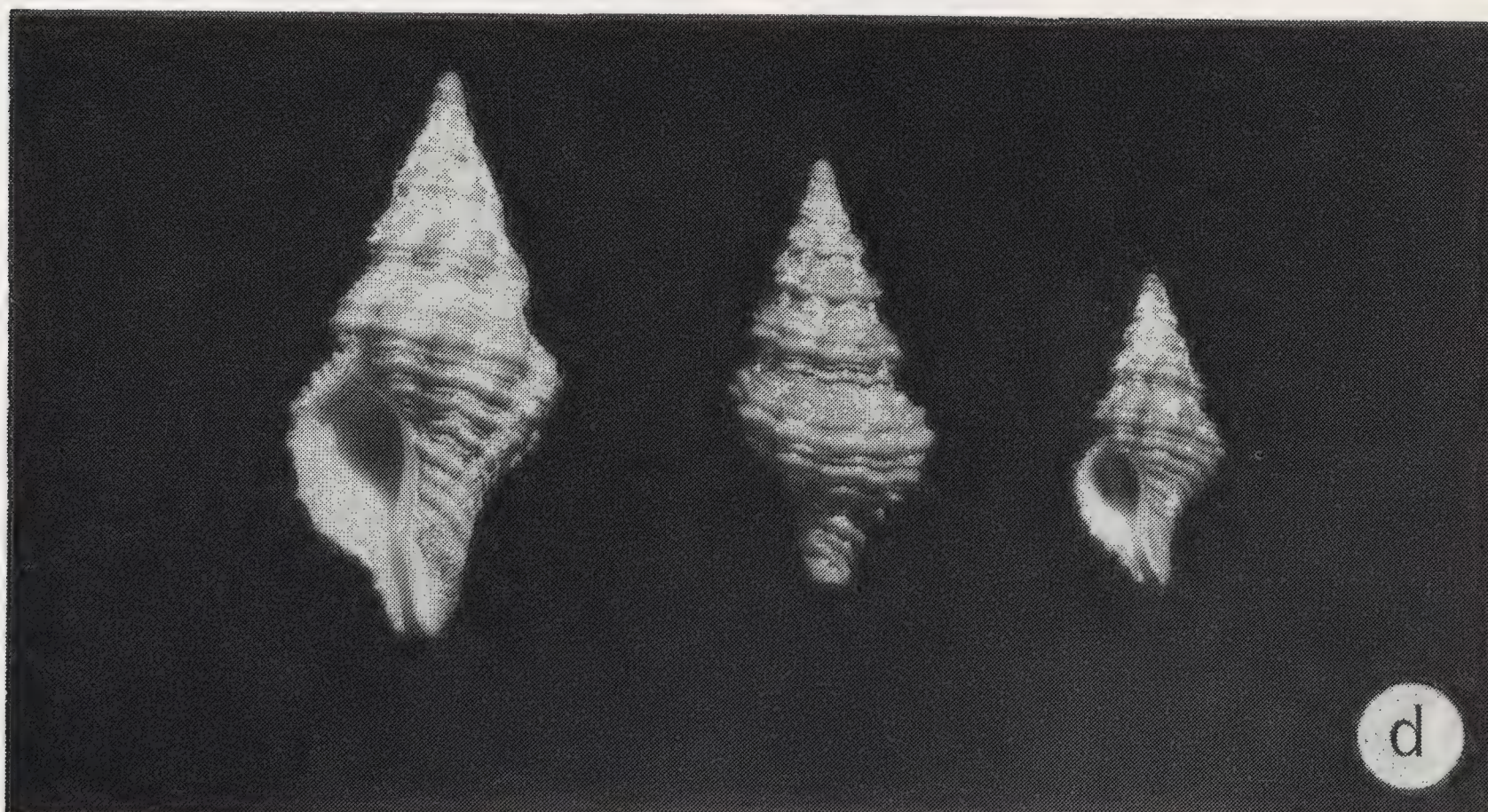
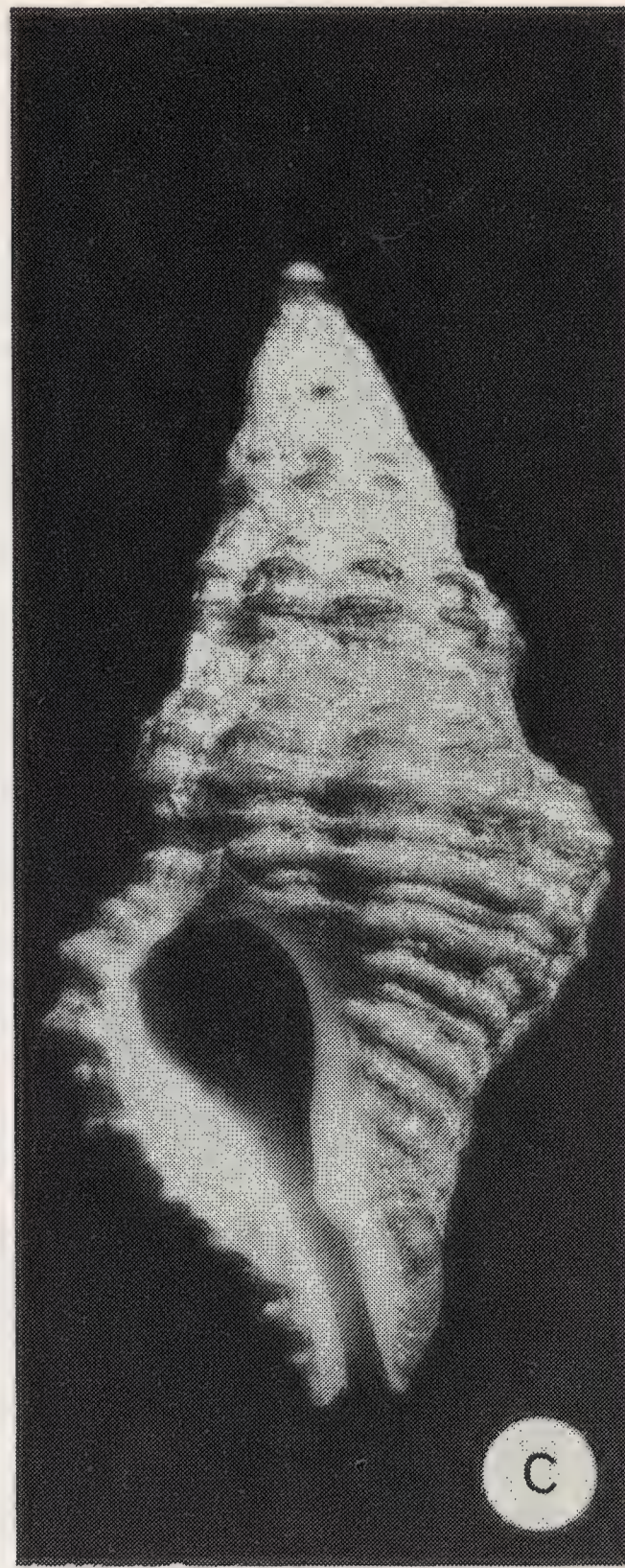


PLATE 18: *Fusinus (Sinistralia) somaliensis* sp. nov. (a) holotype, American Museum of Natural History, New York,  $\times 4$ ; (b-c) paratype, Dr H. G. Lee collection,  $\times 4$ ; (d) paratypes, American Museum of Natural History,  $\times 1.5$ .



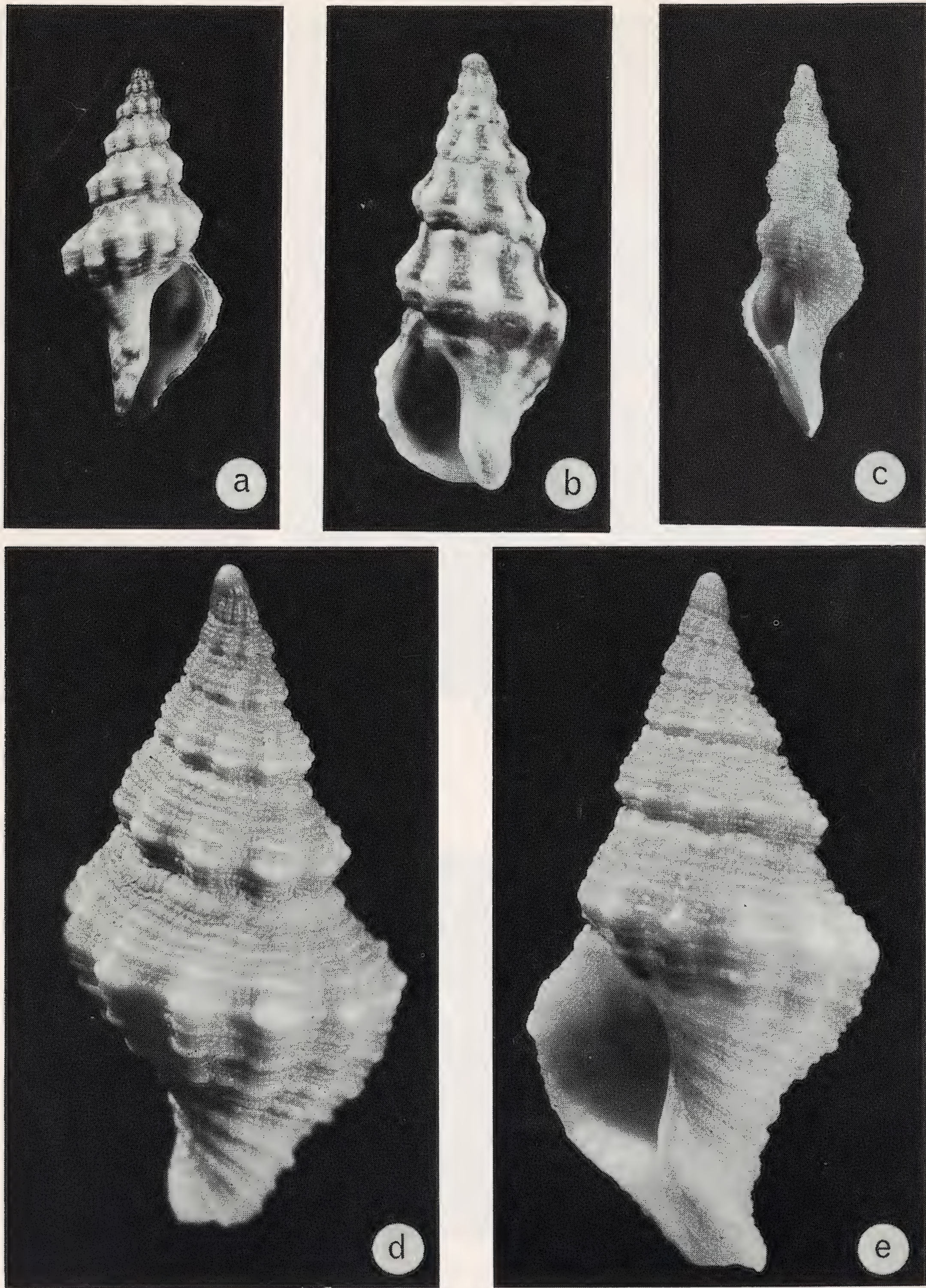


PLATE 19: '*Fusus*' *taylorianus* Reeve (a) figured dextral syntyple (lectotype), (b) sinistral syntyple; (c) *Fusinus* (*Sinistralia*) *elegans* (Reeve), holotype; (d-e) *F. (S.) barclayi* (Sowerby), holotype. All in British Museum (Natural History). All figures approximately  $\times 4$ .



# THE MARINE MOLLUSCA OF KUWAIT, ARABIAN GULF

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*(Accepted for publication, 19 March 1983)*

*Abstract:* This paper deals with the mollusca collected between November 1972 and November 1975 along the coast of Kuwait and its off-shore islands by the authors. All identified mollusca are listed, and information given of the localities, habitats and months found of the living molluscs. A total of 230 gastropods, 5 chitons, 5 scaphopods, 144 bivalves and 1 cephalopod are listed. The collections were made between Khor al Subiyah in the north and Khor al Mufattah in the south.

## HISTORY OF COLLECTING AND RECORDING IN KUWAIT

Little has been written on the mollusca of Kuwait, although there is considerable literature on the Arabian Gulf, the Gulf of Oman and the Arabian Sea (see Smythe 1978). Of all the molluscs listed by Melvill and Standen in their many papers on this area only 10 are noted as being from Kuwait and the other earlier authors record nothing from this region; possibly it was off the more frequented trade routes and far from the submarine cable which was so fruitful a source of molluscs for the Melvill and Standen records. Some collecting was done on the beaches by members of a geological team from Vienna and these were listed as an appendix to their report by Steininger (1968). There are 49 gastropods, 2 scaphopods and 48 bivalves in this list; some of the determinations being incorrect as the author himself declared (personal communication to KRS) as he was given a very limited time to study the shells. Collecting, mostly of empty shells along various beaches, was undertaken by members of the Ahmadi Natural History and Field Studies Group and some preliminary work was done on these by the late H. E. J. Biggs. As a result of his work, 'A Preliminary List of the Mollusca of Kuwait' was published by the Ahmadi Natural History and Field Studies Group in April 1971: this contains some inaccuracies and spelling mistakes. It records 58 gastropods and 12 bivalves. The material sent to the late H. E. J. Biggs is now in the finders' collections, in the British Museum (Natural History) where the Biggs collection is housed, in a collection of representative Kuwait Molluscs belonging to the Ahmadi Natural History and Field Studies Group and some in the possession of one of the authors (KRS) to whom Biggs left his notes and problem shells. This material includes specimens from Bubiyan Island and Failaka Island.

Currently in the press is a handbook of Kuwait Natural History which includes a section on the common molluscs.

## LOCALITIES AND HABITATS

The State of Kuwait lies at the head of the Arabian Gulf from immediately south of the Shatt al Arab to the border with Saudi Arabia (including the Neutral Zone). See Fig. 1.

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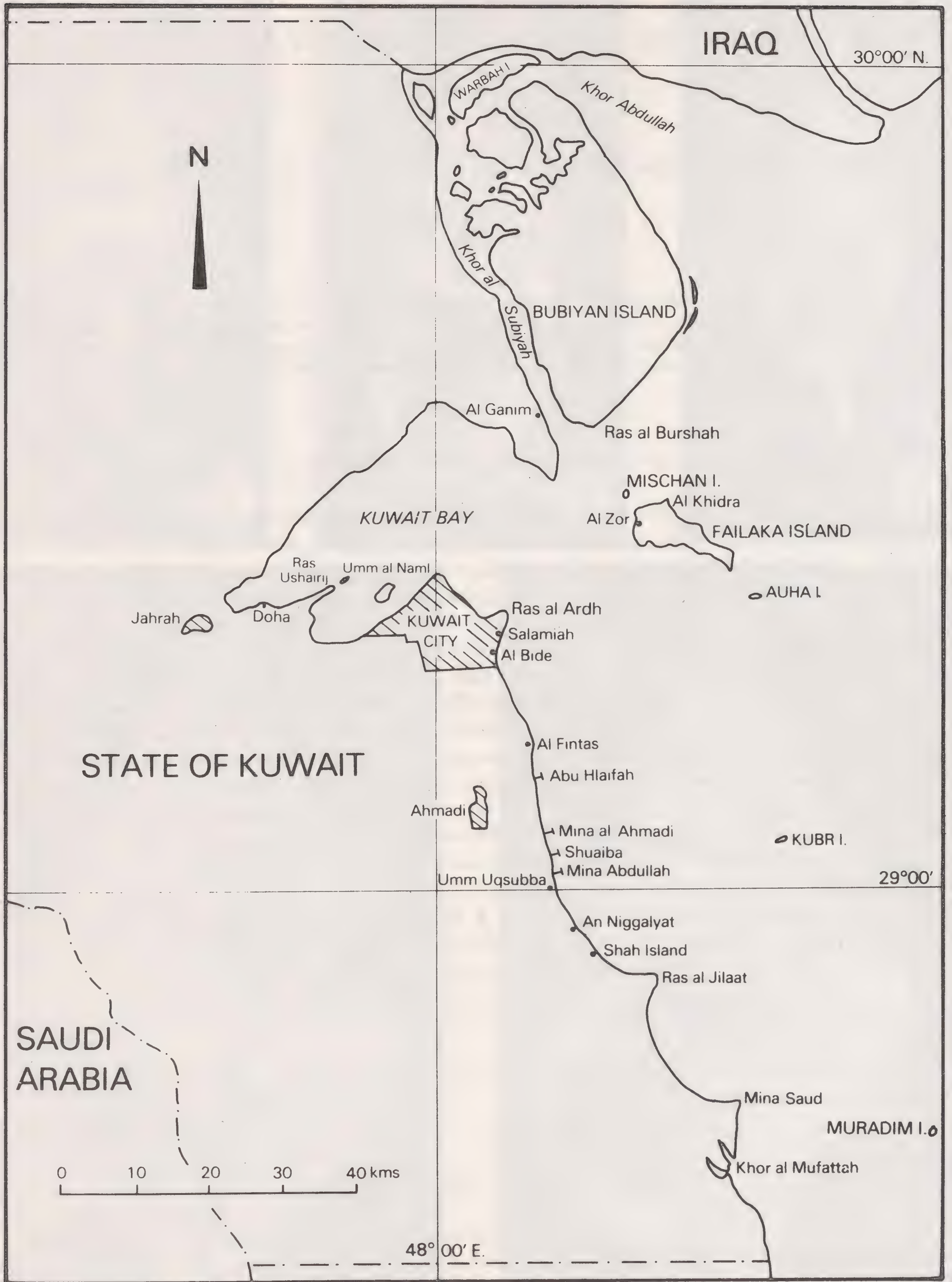


Fig. 1. Map of Kuwait showing collecting localities referred to in the text.



Only limited collection on the off-shore islands was possible due to difficulty of access. No records were obtained from Warbah and Bubiyan Islands during late 1972 to 1975 as they were designated military areas.

For convenience each collecting locality has been allocated a number (which is referred to in the systematic list of Mollusca) and a key to habitats and concentrations, as well as the months of the year when species were found alive, is included. Dead shells along the tide lines were mostly from east coast beaches, and indications of the localities of shells only found dead are given when it was apparent that the molluscs were living in the vicinity, and not collected due to difficulty of access.

- 1 *Khor Al Subiyah*: a sandy foreshore giving way to thick grey, glutinous mud. Very large colonies of *Saccostrea cucullata* and indications that *Placuna placenta* would be found in the mud. Many shells on the beach.
- 2 *Kuwait Bay*: much of it inaccessible due to the military zone.
- 2a *Southern shore of Dohat Khadimah* from Doha to Ras Ushairij: A sharply shelving beach with a large quantity of shell debris about 2 m wide. At 0.0 m tide an extensive area of flat sand and sludgy silt with limestone outcrops and small loose rocks, some in piles, was exposed. The area is crossed by a sewage outfall pipe and conditions are none too salubrious. Many of the rocks are covered by tube worms. At extreme low water the rocks give way to sand and eel grass. There is an abundance of molluscan life, but the number of species is limited.
- 2b *Ras Ushairij North*: Low (1.5 m) rocky cliffs, dropping to flats of silt and sandbars with areas of flat rock and some loose rocks.
- 2c *Ras Ushairij East to Umm Al Naml*: A hard, flat rocky bed, covered with sludge and colonies of *Saccostrea cucullata* and tube worms.
- 2d *A tidal inlet near Umm Al Naml*: accessible at low tide on foot. It is fast flowing with loose rocks and much algae.
- 2e *Umm Al Naml*: A small sandy island surrounded by extensive thick, grey mud flats and occasional sandy patches. The mud is very deep. *Marcia cor* lives here in the mud.
- 3 *Al Bide*: An area protected by low sandstone cliffs above the high water line. Inshore it is sandy, strewn with large boulders. The area slopes gradually in shallow limestone steps to the low water mark, with sandy areas 0.75 m to 1 m deep over the rock, and shallow pools. At 0.0 m tide the beach is approximately 150 m from high to low water marks.
- 4 *Al Fintas*: A sloping beach with a flat outcrop of sandstone, covered with areas of sand. A concentration of shell debris along the tide lines.
- 5 *Abu Hlaifah*: At the northern end of this location a sandy area merges into a flat limestone mass, protruding into the sea. The northern side of this is raised into a shallow cliff about a metre in height, the southern side is a sand bar. The area is dotted with loose rocks. The southern end of the location has a sandy beach which merges into an area of limestone outcrops with numerous pools, and then sand again to the low water mark. At extreme low water coral could be seen.
- 6 *Shuaiba*: Coarse sand over limestone rock forms sandy pools and rocky mounds with loose rocks.
- 7 *Umm Uqsubba*: On the north is a breakwater of large rocks, the top of which is exposed at high tide. There is a sandy beach with limestone outcrops and about 30 m out from the low water mark sandbars are exposed at low tide.
- 8 *An Niggalyat*: A shallow, curving bay, with a shelving sandy beach descending to a flat area of limestone, overlaid with sand in places. Near the low tide mark are large patches of sand and eel grass, and a series of sand banks separated by channels and shallow pools. The rock and patches of live coral outcrop in places. At 0.0 m tide the area extends seawards for more than 1.5 km.
- 9 *Ras Al Jila'at*: The collecting localities here are on either side of a rocky point leading out



to a sandbar. Northwards is a large area of exposed limestone, interspersed with sandy pools which ends abruptly about 200 m offshore. Live coral is common at the edge here. To the south is an expanse of sand with occasional piles of boulders. There is a large quantity of shell debris along the tidelines.

- 10 *Khor Al Mufattah*: A wide sea beach with extensive sand flats and sand bars at low tide.
- 11 *Mufattah Creeks*: A series of salt water creeks, bounded by rocks nearer the sea and salt flats (*subkha*) further inland, where the creeks broaden out with expanses of grey silt exposed at low tide. All the arms of the creeks have deeper central channels and, in places, low growths of weed. At the mouth of the creeks is a good concentration of shell sand.
- 12 *Failaka Island*: A moderately large, waterless island with a small population and some Greek ruins.
- 12a At *Al Khidra* the shore is of flat rock, with patches of greyish muddy silt, bounded by low cliffs.
- 12b At *Al Zor* are beaches of coarse sand sloping to low rocky outcrops with pools and sand bars. Here were large concentrations of shell sand.
- 13 *Kubr Island*: off Shuaiba.
- 14 *Garu Island*: off Mina Saud (east north east)
- 15 *Muradim Island*: south of Mina Saud. These are small, waterless islands about 100×200 m and not exceeding 20 m in height. There are sloping sandy beaches, composed of shell and coral debris and some flat, layered outcrops of sandstone rock. Living corals, almost never exposed at low water, surround the islands.

The construction during the last 38 years of the refining, industrial and port complexes of Mina Al Ahmadi, Shuaiba, Mina Abdullah and Mina Saud, and the growth of Kuwait City have caused considerable changes to the original coastline, and marine fauna in general. Specifically, a number of areas changed radically during the collecting period, due either to the development of areas for recreational purposes (Al Bide, Salamiah and Abu Hlaifah) or the effects of major oil spillage and subsequent anti-pollution measures which affected all areas south of Ras al Jila'at.

## TIDES

Tides vary from -0.2 m below mean sea level to 2.9 m above mean sea level at Mina al Ahmadi (Lat. 29°04'N Long. 48°10'E). Heights are referred to the datum of the largest scale Admiralty chart No. 1223. Heights of both high and low water are considerably affected by the prevailing winds.

## FIELD OBSERVATIONS

During the collecting period covered by the authors a total of 160 field trips were undertaken. Khor al Subiyah 2 trips, Kuwait Bay—a) 8 trips, b) 7 trips, c) 7 trips, d) 3 trips, e) 2 trips, Al Bide 15 trips, Al Fintas 7 trips, Abu Hlaifah 29 trips, Shuaiba 9 trips, Umm Uqsubba 10 trips, An Niggalyat 17 trips, Ras Al Jila'at 15 trips, Khor Al Mufattah 9 trips, Mufattah Creeks 8 trips, Failaka Island a) 2 trips, b) 3 trips, Kubr Island 4 trips, Garu Island 1 trip, Muradim Island 1 trip.



Prior to 7 April 1974 gastropods only were collected or observed. The majority of the species listed were found living in the intertidal zone.

*Species not found in the inter-tidal zone*

*Turbo radiatus*; collected by diving 1–2 m.

*Pteria marmorata*; collected live by diving in deep water, collected dead washed up at An Niggalyat on *Gorgonia* sp.

*Pyrene atrata*; found live adhering to *Pinctada radiata* brought up from about 2.5 m. Dead specimens were common on the tide line.

*Tibia insulaechorab*, *Bursa spinosa*, *Murex* n.sp. K 1059; were brought up in the trawl nets of a shrimp trawler of the Kuwait Fishing Co. in the presence of one of the authors (DTG) in about 50 m of water between Seas Island Oil Terminal and Kubr Island.

*Teredo* sp., *Vanikoro cancellata* *Amalthea tricostrata* *Aspidopholas obtecta*; were on or in timber from a pier at Shuaiba Harbour collected by Mr. H. Onfermann. The timber was taken from approximately 10 m depth and had been in the water for about 2 years.

*Aplysia cornigera* was found swimming in weed and eel grass at the extreme low tide line at Ras Ushairij.

*Bullaria ampulla*, *Tibia insulaechorab* juvenile, *Phalium pila*, *Cucullaea concamerata*, *Cardita ffinchi*, *Lutraria philippinarum*, *Laevicardium papryraceum*, *Meropesta nicobarica* and *Laternula* n.sp. were only collected live as a result of severe storms which washed them into the inter-tidal zone. *Euchelus bicinctus* was found on rock, but also on weed washed up after a storm.

*Species appearing to show seasonal tendencies*

During the winter of 1972/73 numbers of juvenile *Strombus decorus persicus* were seen in large colonies which covered several square metres. Also at this time large numbers of *Cypraea turdus* were observed, all with mantle retracted and of dark colouring. These large concentrations were not seen again until the winter of 1974/75. Dark coloured specimens of *Cypraea turdus* appeared to be healthy, whereas pale specimens tended to be parasitised by worms inside the dorsal surface of the shell.

*Inquisitor griffithi*, *Nassarius marmoreus* and the *Mitra* spp which were common in winter, had by mid-April retreated into deeper water. During the winter of 1973/74 *Bullia tranquebarica*, *Ancilla* spp and *Naticids* were common, but were not seen again until 1.1.75.

During each summer, when sun temperatures at noon were up to 62°C (146°F), large colonies of *Cerithium caeruleum* and *Clypeomorus morus* appeared in shallow water (up to 0.40 m) on sandstone.

Relatively large populations of *Fusinus townsendi* were seen up to May 1973, but were not seen again until June 1974.

Numerous egg collars of *Neverita didyma* were seen on sand bars in conjunction with live animals during February 1975.

*Cypraea turdus* was observed laying eggs on 6.5.74.

*Rapana bulbosa* was observed mating on 17.5.73.

*Thais mutabilis* and *Thais tissoti* were observed laying eggs 22.4.74.

*Cronia fiscella* was observed laying eggs inside dead double *Circe* shells in Khor Al Mufattah Creek on 8.8.75. (six separate individuals).

*Cephalopoda* egg clusters (possibly *Sepiella inermis*) were observed in February and March 1975.

*Other observations*

*Clypeomorus morus* was almost always found in the open with *Cerithium caeruleum*, on the other hand, *Clypeomorus bifasciatus* and *Cerithium scabridum* were found in the shade under stones. The striped form of *Clypeomorus bifasciatus* was most common in sand around Kuwait Bay,



*Triphora corrugata* and *Seila* K 1100 were always found living together in small colonies in approximately equal numbers, suspended by mucous threads, under rocks.

*Crepidula walshi*, sometimes in colonies, was almost invariably found inside empty shells which were occupied by hermit crabs; there were usually one or two sea anemones adhering to the outside of the shell. The association of *Crepidula walshi* and hermit crabs has been described in detail by Yipp (1980). Occasionally specimens were found inside the aperture of live *Hexaplex kuesterianus* and *Rapana bulbosa*. The most common shells inhabited were *Hexaplex kuesterianus*, *Rapana bulbosa*, *Neverita peselephanti*, *Fusinus townsendi* and *Ancilla castanea*.

*Vermetus* sp. K 1355 were coarsely sculptured, and the animal had blue siphons.

A small colony of juvenile *Schizochiton jousseaumei* was found on a live *Pinna muricata* in the fast flowing tidal channel at Umm Al Naml.

*Dentalium longitrorsum* was found in a sub-fossil state at Shuaiba, no fresh specimens were found.

Dead valves of *Placuna placenta* and *Solen capensis* were very common at Khor Al Subiyah but no live specimens could be obtained due to the danger of being trapped in the mud. Some juvenile *Solen capensis* were collected, but these appeared to have been washed up, and were not active.

*Scintilla lavardi* was always found living in a clear jelly, either singly or with other individuals.

*Gafrarium pectinatum* was only found live inside double valves of dead *Chama pacifica*.

*Irus irus* and *Venerupis deshayesei* were found inside double valves of dead *Plicatula plicata*. *Venerupis deshayesei* was not otherwise found live. *Meretrix meretrix* dug up from 0.20–0.30 m in sandy silt at Khor Al Mufattah Creek were all live, and each contained a small (10 mm) greenish-white crab living within the shell near the hinge.

Two specimens of the white form of *Ancilla ovalis* were found.

#### COMMENTS ON SPECIES IDENTIFICATION

The taxonomic order followed in the list of Mollusca is that of Wenz and Zilch (1938–1961) modified by Taylor and Sohl (1962) for the Gastropoda, and Moore (1969) for the Bivalvia.

*Machroschisma elegans* Preston—these shells agree with a specimen labelled thus in the general collection of BMNH but we have not located the type nor the description, so it may be one of Preston's notorious 'New species' (Dance 1966, pp. 223–224).

*Epitonium* cf *replicatum* does not exactly match the lectotype of *Scalarina replicata* in the BMNH but appears to be the same as one of the para-lectotypes (both the para-lectotypes are not the same species as the lectotype.) There are specimens of *Epitonium* cf *replicatum* labelled *Scala replicata* in the general collection from the Maldives Islands and from Arabia which exactly match our shells.

*Murex* sp. K 1059 is believed to be a new species currently being studied and described by Dr. Ponder.

Two Dorids remain unidentified; one, K 1377 was blackish–violet with a frilly double–edged mantle; the other, K 1449 was a pale milky–white with bluish–violet spots, and yellow rhinophores and tentacles.

A specimen of ?*Cyclichna* K 1337 was frequent in the shell sand from Failaka Island only. As the live animal was not found a definite determination of genus is not possible.

Molluscs recorded live for the first time to the best of our knowledge: *Eunaticina pomatiella*, *Phenacolepas omanensis*, *Pyrene atrata*, *Tornatina involuta*, *Tornatina persiana*.



## CONCLUSIONS

Molluscan populations were high on the whole, though the offshore islands of Kubr, Garu, and Muradim had a limited fauna. Biggs's records from Bubiyan of dead shells show a limited fauna of the type to be expected from an area of dense mud flats. Failaka Island had a large population of species, many different from those found on the mainland.

Some families are notable for their absence:

- (i) There are no species of Patellacea—we have found no records of this superfamily occurring down the Arabian coast before Ras Al Khaimah. Suitable habitats are not lacking. This observation also applies to the giant chiton *Acanthopleura haddoni* (Winckworth)
- (ii) Littorinidae are poorly represented, not only in the Arabian Gulf, but also in the Gulf of Oman, as far west as Salalah, where true Indian Ocean conditions prevail.
- (iii) *Ancilla* species are represented in Kuwait, but surprisingly no *Oliva*, especially *Oliva bulbosa*, so common virtually everywhere else.
- (iv) There are only three species of *Cypraea*, though we have reports of findings of dead *C. pulchra* and *C. arabica*.
- (v) No species of Conidae were found, but there has been a recent report of a dead *Conus tessalatus* being found (ANH & FSG Newsletter No 21, August 1982). This is probably an accidental, as it is only reported from considerably further south.

A number of Indian Ocean species occur which do not appear to live further south on the Arabian coast, although recorded from Iran and the Mekran Coast. (Personal observations, and see the lists in Smythe 1972, Smythe 1979, Biggs 1973, Biggs and Grantier 1960, Haas 1952, Haas 1954, Basson et al 1977 and Tadjalli-Pour 1974 and personal communication). These species are denoted by the letter 'K' on the taxonomic list.

It is not thought that this is due to the absence of suitable habitats, as these occur throughout the Gulf (though not so much in the area of the Qatar peninsula and Abu Dhabi). It may be due partly to the current which flows through the Strait of Hormuz up the Iranian side of the Gulf to Iraq, and then spirals southwards in an anti-clockwise movement with decreasing force. This factor probably influences the spread northwards of the Indian Ocean species, but limits their expansion down the Arabian Coast. Another important factor may be the increasing salinity of the sea water as it spirals down the coast, evaporating in the shallows, and the increasing number of large shallow 'subkha' and intertidal creeks with salinities of up to 79‰ (Salinity of sea water off Shuaiba is about + or - 38‰). A further point to be born in mind in drawing conclusions from these faunal lists is that the current one is the result of a period of three years of continuous observation by the authors; Biggs and Smythe lists have been based on erratic collecting by certain reliable friends and periodic visits by one of the authors over a limited time. Hass's lists (which contain errors) were on short visits to some places only; Basson et al. contain many unidentified species (some of which may occur in Kuwait).

A total in excess of 435 species of molluscs was found, many by sifting through shell sand collected along the tide lines. 230 gastropods, 5 chitons, 5 scaphopods, 144 bivalves and 1 cephalopod have been identified and are listed here. At least 50 gastropods and 16 bivalves not listed here remain to be identified. 77 species are listed as not occurring further south.



TABLE 1

List of species found during the collecting period of this paper

Species	Localities		Months found	
<b>Gastropoda</b>				
Scissurellidae				
<i>Scissurella peilei</i> Winckworth	R	—		
<i>Scissurella jacksoni</i> Melvill 1904	R	—		
Fissurellidae				
<i>Emarginula incisura</i> A. Adams 1884	R	—		
<i>Emarginula clathrata</i> Pease 1862	R	2d	H	II, IX
<i>Diodora funiculata</i> (Reeve 1850)	F	2d, 7, 8	H	I–XII
<i>Diodora imbricata</i> (Sowerby 1862)	O	5, 8	H	III, IV
<i>Diodora rueppelli</i> (Sowerby 1834)	R	3, 7, 10	H	IV–VI
<i>Diodora bombayana</i> (Sowerby 1862)	R	2d	H	II, IX
<i>Machroschisma elegans</i> Preston	R	—		
Trochidae				
<i>Turcica stellata</i> A. Adams 1863	O	—		
<i>Euchelus asper</i> (Gmelin 1791)	C	2a, 3, 5, 6, 8, 9, 12b	H	I–XII
<i>Euchelus bicinctus</i> (Philippi 1849)	O	2d, 9	HW	II, IV
<i>Euchelus foveolatus</i> (A. Adams 1851)	F	2d	H	II, IX
<i>Minolia biangulosa</i> (A. Adams 1854)	F	—		
<i>Gibbula declivis</i> (Førsskal 1817)	R	—		
<i>Trochus erythraeus</i> Brocchi 1821	F	2d, 3–9 12b	H	I–XII
<i>Clanculus pharaonis</i> (Linnaeus 1758)	O	—		
<i>Clanculus scabrosus</i> (Philippi 1850)	R	12b	H	XI
<i>Minolia solanderi</i> (Philippi 1851)	O	—		
<i>Minolia gradata</i> Sowerby 1895	F	—		
<i>Minolia holdsworthiana</i> G. & H. Nevill 1871	R	—		
<i>Minolia variabilis</i> A. Adams 1873	R	—		
<i>Monilea obscura</i> (Wood 1828)	A	1, 2a, 2b, 2d, 3—11, 12b, 13	HS	I–XII
<i>Monodonta vermiculata</i> (Fischer 1874)	F	3, 5, 8, 9, 13	H	I, III–V, VII
<i>Ethalia carneolata</i> Melvill 1897	R	—		
<i>Umbonium vestiarius</i> (Linnaeus 1758)	A	2a, 2b, 3–10	S	I–XII
Stomatellidae				
<i>Stomatia phymotis</i> Helbing 1779	R	5	H	V
<i>Stomatella duplicata</i> Sowerby 1854	R	—		
<i>Stomatella sulcifera</i> Lamarck 1823	R	—		
<i>Gena planulata</i> A. Adams 1850	KR	—		
Cyclostrematidae				
<i>Cyclostrema ocrinum</i> Melvill & Standen 1901	R	—		
<i>Cyclostrema novemcarinatum</i> Melvill 1906	R	—		
<i>Cyclostrema quadricarinatum</i> Melvill & Standen 1901	F	—		
<i>Cyclostrema solariellum</i> Melvill & Standen 1901	R	—		

LEGEND: *Localities*: see list of localities and the numbers allocated to them (p. 311).

*Frequency*: A, abundant; C, common; F, frequent; O, occasional; R, rare. The letter K preceding the frequency letter indicates that the species does not occur further south on the Arabian Coast.

*Habitat*: H, on, in or under rock or hard substances; M, mud; S, sand; W, weed; +, other habitats (discussed in the text); —, found dead; mostly in debris along tide lines of the east coast. Where localities of living animals were certain these have been stated.

*Months of the year* when living animals were observed in situ are shown as I to XII (I=January, II=February, etc.). Unidentified living species are annotated by our reference number e.g. 'K1059'.



Species	Localities		Months found	
Turbinidae				
<i>Turbo coronatus</i> Gmelin 1791	A	2a,2b,2d,3–12a,13	H	I–XII
<i>Turbo radiatus</i> Gmelin 1791	O	13–15	H	V,VI
<i>Leptothyra filifera</i> (Deshayes 1863)	F	—		
Phasianellidae				
<i>Phasianella solida</i> (Born 1778)	O	—		
<i>Tricolia fordiana</i> Pilsbry 1888	O	—		
Neritidae				
<i>Smaragdia souverbiana</i> (Montrouzier 1863)	R	—		
<i>Nerita albicilla</i> Linnaeus 1758	R	7,15	H	IV,VI
Phenacolepadidae				
<i>Phenacolepas arabicus</i> Rueppell in Thiele 1909	R	—		
<i>Phenacolepas evansi</i> Biggs 1973	R	—		
<i>Phenacolepas omanensis</i> Biggs 1973	O	2a	H	II,III,IV
Mesogastropoda				
Littorinidae				
<i>Nodilittorina millegrana</i> (Philippi 1848)	A	2a,2b,3,7,8,11,12a,15	H	I–XII
<i>Peasiella isseli</i> (Semper in Issel 1869)	F	2b,3	H	II,III,IV
Rissoidae				
<i>Cingula vitrea</i> (Montagu 1803)	R	—		
<i>Cingula tiberiana</i> (Issel 1869)	C	—		
<i>Iravadia annulata</i> (Dunker 1860)	F	2d	H	II–IX
<i>Pyramidelloides miranda</i> (A. Adams 1861)	F	—		
<i>Amphithalamus microthyra</i> (von Martens 1880)	R	—		
<i>Amphithalamus alphesboei</i> Melvill 1912	R	—		
<i>Rissoina distans</i> (d’Anton 1839)	R	2d,4	H	II
<i>Rissoina seguenziana</i> (Issel 1869)	C	—		
<i>Rissoina clathrata</i> (A. Adams 1851)	O	—		
<i>Iraquirissoa xanthias</i> (Watson 1886)	KO	—		
<i>Stenothyra iraqensis</i> Dance & Eames 1966	R	—		
<i>Homalogyra atomus</i> (Philippi 1850)	R	—		
<i>Iraquirissoa aristaei</i> Melvill 1912	R	—		
Architectonicidae				
<i>Pseudomalaxis</i> cf <i>zancleus</i> (Philippi 1844)	R	—		
Turritellidae				
<i>Turritella fultoni</i> Melvill 1898	O	—		
<i>Turritella auricincta</i> von Martens 1882	O	—		
<i>Turritella torulosa</i> Kiener 1843	R	—		
Vermetidae				
<i>Vermetus sulcatus</i> Lamarck 1818	C	2a,3,5,8,9	H	I–XII
<i>Vermetus</i> sp.K1355	F	2a,5,8,15	H	I–XII
Planaxidae				
<i>Planaxis sulcatus</i> (Born 1778)	C	2a,2c,3,5,11,12a,15	H	I–XII



Species	Localities		Months found	
Potamididae				
<i>Pirenella conica</i> (Blainville 1826)	O	—		
<i>Cerithidea cingulata</i> (Gmelin 1791)	A	1,2a,2e,3,10–12a	MS	I–XII
Finellidae				
<i>Finella pupoides</i> A. Adams 1860	C	—		
<i>Finella purpureoapicata</i> Preston 1905	A	—		
<i>Finella scabra</i> A. Adams 1860	C	—		
<i>Scaliola arenosa</i> A. Adams 1869	A	—		
Dialidae				
<i>Diala goniocheila</i> (A. Adams 1840)	O	—		
<i>Diala semistriata</i> (Philippi 1849)	R	—		
<i>Diala sulcifera</i> (A. Adams 1862)	C	—		
<i>Alaba virgata</i> (Philippi 1849)	F	—		
Cerithiidae				
<i>Bittium</i> sp. K1194	R	2a,5	H	III
<i>Rhinoclavis kochi</i> (Philippi 1848)	F	5,6,8	S	VII,IX,XII
<i>Cerithium caeruleum</i> Sowerby 1865	A	2a,3–9,11,13,15	SH	I–XII
<i>Cerithium pingue</i> A. Adams 1855	KR	10	W	I
<i>Cerithium scabridum</i> Philippi 1848	C	3,5,7,9,12a	S	I–XII
<i>Clypeomorus bifasciatus</i> (Sowerby 1855)	A	2a,2b,3–9,11,12a,12b	SH	I–XII
<i>Clypeomorus morus</i> (Lamarck 1822)	A	2a,3–9,12a,13,15	SH	I–XII
Cerithiopsidae				
<i>Seila</i> sp. K1100	O	2a,5	H	III
<i>Cerithiopsis semipicta</i> Gould 1861	O	2a,5	H	I,II,III,IX
<i>Cerithiopsis hinduorum</i> Melvill 1898	O	—		
Triphoridae				
<i>Triphora acicula</i> Issel 1869	KO	—		
<i>Triphora acuta</i> (Kiener 1841)	R	—		
<i>Triphora aegle</i> (Jousseaume 1884)	KO	—		
<i>Triphora ?capensis</i> Bartsch 1915	KR	—		
<i>Triphora cingulata</i> A. Adams 1851	F	—		
<i>Triphora corrugata</i> Hinds 1843	F	5	H	II,III,IX,XII
<i>Triphora</i> cf <i>distinctus</i> Deshayes 1863	KO	—		
<i>Triphora incolumnis</i> Melvill 1918	R	—		
<i>Triphora maxillaris</i> Hinds 1843	KR	—		
<i>Triphora perversa</i> (Linnaeus 1758)	C	—		
<i>Triphora tristoma</i> (Blainville 1824)	KR	—		
Epitoniidae				
<i>Epitonium robillardi</i> (Sowerby 1844)	R	—		
<i>Epitonium aculeatum</i> (Sowerby 1844)	O	—		
<i>Epitonium alatum</i> (Sowerby 1844)	KR	—		
<i>Epitonium deificum</i> (Melvill 1903)	F	—		
<i>Epitonium hidryma</i> (Melvill 1899)	KR	—		
<i>Epitonium simplex</i> (Sowerby 1894)	C	—		
<i>Epitonium</i> cf <i>replicatum</i> (Sowerby 1844)	KR	—		
Fossaridae				
<i>Fossarus thelacme</i> Melvill 1904	KR	—		
Vanikoridae				
<i>Vanikoro cancellata</i> (Lamarck 1844)	KR	16	H	II
<i>Vanikoro expansa</i> Sowerby 1901	O	—		
<i>Vanikoro quoyana</i> Angas 1867	R	—		



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Species	Localities		Months found	
Amaltheidae				
<i>Amalthea tricostata</i> (Gmelin 1791)	R	6	H	II
Calyptraeidae				
<i>Calyptraea pellucida</i> Reeve 1859	C	—		
<i>Crepidula (Siphopatella) walshi</i> Hermansson in Reeve 1859	F	8,9	+	I,III,IV,VI,VII
Xenophoridae				
<i>Xenophora corrugata</i> (Reeve 1843)	O	—		
Strombidae				
<i>Terebellum terebellum</i> (Linnaeus 1758)	R	6	S	II
<i>Tibia insulaechorab</i> Roeding, 1798	KR	3,16	+S	V,VIII
<i>Strombus decorus persicus</i> Swainson 1821	A	3–11,13	S	I–XII
<i>Strombus fusiformis</i> Sowerby 1842	O	—		
Naticidae				
<i>Natica lineata</i> (Roeding 1798)	O	3,4,7,9,10	S	I,III–VI,X,XI
<i>Natica pulicaris</i> Philippi 1851	KF	3–5,6	S	I,IV,X,XI
<i>Natica trailli</i> Reeve 1855	R	3	S	II
<i>Natica vitellus</i> Linnaeus 1758	KO	—		
<i>Neverita didyma</i> (Roeding 1798)	O	3,4,6,8,9	S	I,II,VI,XI,XII
<i>Neverita peselephanti</i> (Link 1807)	KO	—		
<i>Eunaticina papilla</i> (Gmelin 1791)	R	6	S	XI
<i>Eunaticina pomatiella</i> Melvill 1892	R	5,6,9	S	II,III
<i>Ectosinum planatum</i> (Recluz 1843)	KR	—		
<i>Polinices tumidus</i> (Swainson 1840)	R	—		
Cypraeidae				
<i>Cypraea gracilis</i> Gaskoin 1848	R	8,15	SH	II,VI,XII
<i>Cypraea lentiginosa</i> Gray 1825	O	8	SH	II,III,XI,XII
<i>Cypraea turdus</i> Lamarck 1810	C	3–10	S	I–II
Ovulidae				
<i>Ovula concinna</i> Adams & Reeve 1848	KR	—		
<i>Prosimnia trailli</i> A. Adams 1855	KR	9	W	IV
Cassidae				
<i>Phalium pila</i> (Reeve 1848)	R	8,9	S	II,XII
Bursidae				
<i>Bursa echinata</i> (Link 1807)	KR	16	+	V
Ficidae				
<i>Ficus subintermedia</i> (d'Orbigny 1852)	R	—		
Muricidae				
<i>Rapana bulbosa</i> (Solander 1817)	F	3–9	S	I–XII
<i>Murex scolopax</i> Dillwyn 1817	F	3,5,7–10	SH	I–XII
<i>Murex</i> sp. K1059	R	16	+	V
<i>Hexaplex kuesterianus</i> (Tapparone Canefri 1875)	C	3–10,12b	H	I–XII
<i>Homalocantha rota</i> (Mawe 1823)	R	—		
Thaididae				
<i>Thais mutabilis</i> (Link 1807)	F	3,5,7–11,12b	H	I–XII
<i>Thais savignyi</i> (Deshayes 1844)	C	3–11,13,15	H	I–XII
<i>Thais tissoti</i> Petit 1853	F	3,5–9	H	I–XII
<i>Cronia fiscella</i> (Gmelin 1791)	A	2a,3–10,12b,13	H	I–XII



Species	Localities		Months found	
Columbellidae				
<i>Columbella varians</i> Sowerby 1832	KO	—		
<i>Mitrella blanda</i> (Sowerby 1844)	A	1,2a,3–10,12a,12b	MS	I–XII
<i>Mitrella cartwrighti</i> (Melvill 1897)	C	—		
<i>Pyrene atrata</i> (Gould 1860)	R	8	+	VI
<i>Pyrene phaula</i> (Melvill & Standen 1901)	C	—		
Nassariidae				
<i>Bullia tranquebarica</i> (Roeding 1798)	KO	3	S	I,XI
<i>Nassarius arcularius plicatus</i> (Roeding 1798)	A	2a,3–11,12b	MS	I–XII
<i>Nassarius albescens gemmuliferus</i> (A. Adams 1852)	KF	3–6,8	S	I–IV,X–XII
<i>Nassarius marmoreus</i> (A. Adams 1851)	KF	3,4,8,9	S	I,II,VI
<i>Nassarius glans</i> (Linnaeus 1758)	KR	—		
<i>Nassarius frederici</i> (Melvill 1901)	KC	—		
<i>Nassarius mammiliferus</i> (Melvill, 1897)	KF	—		
Fascioliariidae				
<i>Fusinus townsendi</i> (Melvill 1899)	F	3–5,7–9	SH	I–VII
Olividae				
<i>Ancilla castanea</i> (Sowerby 1830)	F	3–9	S	I–XII
<i>Ancilla farsiana</i> Kilburn 1981	KC	—		
<i>Ancilla ovalis</i> (Sowerby 1859)	F	3–6,8–10	S	I,IV–VI,X,XI
Mitridae				
<i>Mitra bovei</i> Kiener 1839	O	8,9	S	V,VIII,XI
<i>Mitra malcolmensis</i> Melvill & Standen 1901	KF	—		
<i>Cancilla circula</i> (Kiener 1839)	KR	—		
<i>Neocancilla clathrus</i> (Gmelin 1791)	F	3,4,6	S	I,II,VI,X
Vexillidae				
<i>Pusia osiridis</i> (Issel 1869)	KO	3–5	S	I,II,VI,XII
Cancellariidae				
<i>Trigonostoma costifera</i> (Sowerby 1833)	KR	6	S	I
<i>Cancellaria melanostoma</i> Sowerby 1833	KR	—		
Marginellidae				
<i>Gibberula</i> cf. <i>mazagonica</i> (Melvill 1892)	F	—		
<i>Gibberula suizensis</i> (Issel, 1869)	C	—		
<i>Cypraeolina isseli</i> (G. & H. Nevill 1875)	R	—		
Turridae				
<i>Clathurella martensi</i> G. & H. Nevill 1875	R	2d	H	II
<i>Cythara striatella</i> Smith 1884	R	—		
<i>Drillia booleyi</i> Melvill & Sykes 1897	F	—		
<i>Epidirona multiseriata</i> (Smith 1877)	R	—		
<i>Etrema lemniscata</i> (G. & H. Nevill 1875)	KR	2d,9	H	II,VIII,IX
<i>Eucythara edithae</i> (Melvill & Standen 1901)	KF	—		
<i>Eucythara elevata</i> Smith 1844	O	—		
<i>Eucythara lyrica</i> (Reeve 1846)	O	7,8,10	S	I,III,VIII
<i>Kermia foraminata</i> (Reeve 1845)	KF	—		
<i>Inquisitor griffithi</i> (Gray 1834)	O	4–6	S	I,IV,VI,X
<i>Lienardia mighelsi</i> Iredale & Tomlin 1917	KR	—		
<i>Mangelia albolabrata</i> Smith 1882	KO	—		
<i>Mangelia horneana</i> Smith 1844	KR	—		
<i>Mangelia horneana</i> var. <i>compar</i> Melvill 1916	R	2d	H	II
<i>Mangelia koweitensis</i> Melvill & Standen 1904	R	—		
<i>Mangelia phaea</i> Melvill & Standen 1901	KR	—		



Species	Localities		Months found	
<i>Mangelia posidonia</i> Melvill 1904	O	—		
<i>Mangelia recta</i> Smith 1888	O	—		
<i>Mangelia townsendi</i> Sowerby 1895	O	3,9	S	I,II,VIII
<i>Splendrillia lucida</i> G. & H. Nevill 1875)	KR	—		
<i>Tomopleura nivea</i> (Philippi 1851)	KR	4	S	II
<i>Vepracula sykesii</i> (Melvill & Standen 1903)	KR	—		
Terebridae				
<i>Terebra livida</i> Reeve 1860	R	—		
<i>Terebra cingulifera</i> Lamarck 1822	R	—		
Acteonidae				
<i>Acteon affinis</i> (A. Adams 1854)	F	2a,3–10	MS	I–IV,VII
<i>Acteon pulchrrior</i> Melvill 1904	O	—		
Ringiculidae				
<i>Ringicula propinquans</i> Hinds 1844	C	—		
Bullaridae				
<i>Bullaria ampulla</i> (Linnaeus 1758)	R	3,9	+	II,XII
Atyidae				
<i>Atys cyclindrica</i> (Helbling 1779)	A	—		
<i>Haminaea vitrea</i> (A. Adams 1858)	O	—		
Retusidae				
<i>Retusa truncatula</i> Bruguière 1792	R	—		
<i>Retusa tarutana</i> Smythe 1979	C	—		
Cyclichnidae				
<i>Tornatina inconspicua</i> H. Adams 1873	R	9	H	VIII
<i>Tornatina involuta</i> (G. & H. Nevill 1871)	R	2d,9	H	VIII
<i>Tornatina persiana</i> Smith 1872	R	2d	H	VIII
<i>Cyclichna pellyi</i> (Smith 1872)	O	—		
? <i>Cyclichna</i> sp K1337	F	—		
Aglaiidae				
<i>Aglaiia</i> cf. <i>nigra</i> von Martens 1879	O	3,10	S	I,II
Aplysiidae				
<i>Aplysia cornigera</i> Sowerby 1869	KR	2a	+	III
Pyramidellidae				
<i>Pyramidella mitralis</i> A. Adams 1855	O	6,8	S	VII,VIII
<i>Pyramidella</i> sp. K1429	R	2d	H	II
<i>Syrnola brunnea</i> (A. Adams 1854)	KC	—		
<i>Syrnola mekranica</i> Melvill & Standen 1904	KA	—		
<i>Eulima gentilomiana</i> Issel 1869	O	—		
<i>Odostomia eutropia</i> Melvill 1899	KC	—		
<i>Odostomia major</i> Melvill & Standen 1901	KO	—		
<i>Kleinella amaena</i> (A. Adams 1851)	R	—		
<i>Chrysallida edgari</i> (Melvill 1896)	R	—		
<i>Turbonilla</i> ? <i>colpodes</i> Melvill 1910	KR	—		
<i>Oscilla faceta</i> Melvill 1904	KC	—		
<i>Syrnola</i> sp. K1335	C	—		
Doridae				
Dorid K1377	R	2a	M	III



Species	Localities		Months found	
Dorid K1449	R	2a	M	VIII
<i>Doriopsilla miniata</i> (Alder & Hancock 1864)	KF	2a,8	MS	II
<i>Dendrodoris nigra</i> (Stimpson 1855)	KO	2a,3,8	MS	II
<i>Chromodoris maculosa</i> (Pease 1871)	KR	2a	M	II
<i>Chromodoris dollfusi</i> Pruvot-Fol 1973	KR	2a	M	VIII
<b>Ellobiidae</b>				
<i>Allochroa bronni</i> Philippi 1846	O	3,8	H	II-IV
<b>Siphonariidae</b>				
<i>Siphonaria laciniosa</i> (Linnaeus 1758)	A	2a,2b,3-9,12a,12b,13,15	H	I-XII
<i>Siphonaria tenuicostulata</i> Smith 1903	C	12a	H	II,XI
<b>Onchidiidae</b>				
<i>Onchidium peronii</i> Cuvier 1805	C	2a,3,5-7,9,10	H	II,VII,VIII
<b>Ischnochitonidae</b>				
<i>Ischnochiton yerburyi</i> Smith 1891	R	2d	H	II,XI
<b>Callistoplacidae</b>				
<i>Callistochiton barnardi</i> Ashby 1931	KR	2d,9	H	II,XI
<b>Schizochitonidae</b>				
<i>Schizochiton jousseaumei</i> Dupuis 1917	KO	2d,3	+H	II,VIII
<i>Schizochiton</i> sp. K1425	R	3	H	I
<b>Chitonidae</b>				
<i>Chilton lamyi</i> Dupuis 1917	R	2d,12b	H	II
<b>Dentaliidae</b>				
<i>Dentalium longitrorsum</i> Reeve 1860	KR	—		
<i>Dentalium eburneum</i> (Linnaeus 1767)	F	—		
<i>Dentalium octangulatum</i> Donovan 1803	F	3,5,8,10	S	V,XII
<i>Dentalium quadrapicale</i> Sowerby 1860	KC	—		
<i>Dentalium tomlini</i> Melvill 1918	R	—		
<b>Bivalvia</b>				
<b>Nuculidae</b>				
<i>Nucula layardi</i> A. Adams 1856	KC	—		
<b>Nuculanidae</b>				
<i>Nuculana brookei</i> (Hanley 1860)	KR	—		
<i>Yoldia nicobarica</i> (Bruguière 1789)	KO	—		
<b>Arcacea</b>				
<b>Arcidae</b>				
<i>Anadara antiquata</i> (Linnaeus 1758)	O	2d,9	MS	II,XII
<i>Anadara ehrenbergi</i> (Dunker 1868)	O	9,10	S	I,II
<i>Anadara secticostata</i> (Reeve 1844)	R	2e	M	II
<i>Anadara uropygmelana</i> (Bory de St. Vincent 1824)	R	—		
<i>Striarca afra</i> (Gmelin 1791)	O	2a,2d,3,5	H	II,III,VII
<i>Striarca tenebrica</i> Reeve 1844	R	—		
<i>Barbatia helbingi</i> (Bruguière 1789)	F	4-6,8-10,15	H	I,II,V,VI,VIII
<i>Barbatia lacerata</i> (Bruguière 1789)	O	8	H	II
<i>Acar plicata</i> Dillwyn 1817	F	2a,2d,3,5,6,8,9,12b	H	I,II,V-IX,XI
<i>Sheldonella cafria</i> Bartsch 1915	R	12b	H	XI
<i>Trisodos tortuosa</i> (Linnaeus 1758)	R	—		



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Species	Localities		Months found	
Cucullaeidae				
<i>Cucullaea concamerata</i> (Martini 1777)	R	9	+	XII
Glycymeridae				
<i>Glycymeris lividus</i> Reeve 1844	O	—		
<i>Glycymeris maskatensis</i> Melvill 1897	F	8	S	II,XII
<i>Glycymeris striatularis</i> (Lamarck 1818)	O	10	S	I
Mytilidae				
<i>Brachidontes</i> sp. K1196	R	2d	H	II
<i>Brachidontes variabilis</i> (Krauss 1848)	O	2a,2d,3,8,12b	H	III,IV,XI,IX
<i>Septifer bilocularis</i> (Linnaeus 1758)	R	2d	H	IX
<i>Modiolus auriculatus</i> Krauss 1848	O	—		
<i>Amygdalum</i> cf <i>japonicum</i> (Dunker 1856)	R	—		
<i>Botula cinnamomea</i> (Lamarck 1801)	C	5,7	H	I–XII
<i>Musculus mirandus</i> Smith	R	—		
<i>Gregariella</i> ? <i>argentea</i> (Reeve 1858)	R	2d	H	IX
<i>Lithophaga</i> cf <i>nasuta</i> Philippi 1846	KR	5	H	I–XII
<i>Lithophaga cumingiana</i> (Reeve 1858)	C	3,5,6,8	H	I–XII
<i>Lithophaga teres</i> Philippi 1846	O	3,5,6	H	I–XII
<i>Lithodomus</i> sp, K1477	O	2d	H	XI
Pinnidae				
<i>Pinna muricata</i> Linnaeus 1758	F	2d,3,5,9,11	S	I,II,V,IX,XII
Pteriidae				
<i>Pinctada radiata</i> (Leach 1814)	F	2a,3–9	H	I–XII
<i>Pteria marmorata</i> Reeve 1847	R	16	+	VIII
Isognomonidae				
<i>Isognomen legumen</i> (Gmelin 1791)	O	5,9,15	H	I,V,VI
<i>Malleus regula</i> (Førsskal 1775)	C	6,8	H	VI,VIII,XI
<i>Malleus</i> sp. K1397	R	2d	H	II
<i>Parviperna dentifera</i> (Krauss 1848)	F	2a,5,7,12a,15	H	II,VI,VII,XI
Pectinidae				
<i>Chlamys crassicostata</i> Sowerby 1842	R	—		
<i>Chlamys ruschenbergeri</i> (Tryon 1870)	F	2a,3–9	WH	I,II,IV,VI,XII
<i>Chlamys senatorius</i> (Gmelin 1798)	R	2b,11	WH	I
Spondylidae				
<i>Plicatula plicata</i> (Linnaeus 1758)	F	3–6,8,12b	H	I–XII
<i>Spondylus gaederopus</i> (Linnaeus 1758)	F	6,8,9,14,15	H	I–XII
<i>Spondylus hystrix</i> Roeding 1798	R	9	H	I–XII
Anomiidae				
<i>Placuna placenta</i> (Linnaeus 1758)	KC	1 dead only	M	II
Limidae				
<i>Lima leptocarya</i> Melvill 1898	R	—		
<i>Lima tenuis</i> (Adams & Angas 1863)	O	—		
Ostreidae				
<i>Alectryonella plicatula</i> (Gmelin 1791)	R	—		
<i>Saccostrea cucullata</i> (Born 1775)	C	1,2a,2c,2d,3,10	MH	I–XII
<i>Crassostrea</i> sp. K1181	O	8	H	XI
<i>Lopha cristagalli</i> (Linnaeus 1758)	R	—		
<i>Ostrea pyxidata</i> Adams & Reeve 1850	R	—		



Species	Localities		Months found	
Lucinidae				
<i>Divaricella cumingi</i> (Adams & Angas 1863)	R	9	S	IV
<i>Anodontia edentula</i> (Linnaeus 1758)	R	—		
<i>Codakia fischeriana</i> (Issel 1869)	R	—		
<i>Bellucina seminula</i> (Gould 1861)	R	—		
<i>Ctena divergens</i> (Philippi 1850)	F	—		
Ungulinidae				
<i>Diplodonta ravayensis</i> Sturany 1901	R	6,9	S	V,XII
Chamidae				
<i>Chama pacifica</i> Broderip 1834	C	2c,3,5,6,8,9,15	H	I–XII
Leptonidae				
<i>Scintilla layardi</i> (Deshayes 1855)	R	2a,11	H	II,VI
<i>Scintilla rosea</i> (Deshayes 1855)	KR	2d	H	II
<i>Galeomma peilei</i> Tomlin 1921	KO	—		
Carditidae				
<i>Beguina gubernaculum</i> (Reeve 1843)	O	5	H	VI,VII
<i>Cardita bicolor</i> Lamarch 1822	O	—		
<i>Cardita ffinchi</i> (Melvill 1898)	R	10	+	VIII
Condylocardiidae				
<i>Cuna majeeda</i> Biggs 1973	R	—		
Cardiidae				
<i>Laevicardium papyraceum</i> (Bruguière 1789)	R	9	S	XII
<i>Trachycardium flavum</i> (Linnaeus 1758)	O	3,4,9	S	I,XII
<i>Trachycardium lacunosum</i> (Reeve 1845)	F	4–6,8,9	S	I,VII,XII
<i>Parvicardium suizensis</i> (Issel 1869)	R	—		
Mactridae				
<i>Mactra glabrata lilacea</i> Lamarck 1818	O	3,5,9	S	I,XII
<i>Lutraria philippinarum</i> Reeve 1854	R	9	+	XII
<i>Meropesta nicobarica</i> (Gmelin 1791)	R	9	+	XII
<i>Ervilia scaliola</i> Issel 1869	A	—		
<i>Spondervilia bisculpta</i> Gould 1861	R	—		
Solenidae				
<i>Solen capensis</i> Fischer 1881	KR	1	M	II
<i>Solen truncatus</i> Wood 1815	KR	—		
<i>Solen cylindraceus</i> Reeve 1843	KR	—		
Tellinidae				
<i>Tellina claudia</i> Melvill & Standen 1907	R	—		
<i>Tellina foliacea</i> (Linnaeus 1758)	R	—		
<i>Tellina inflata</i> Gmelin 1791	O	8,9	S	IV,XII
<i>Tellina nitens</i> Deshayes 1854	R	—		
<i>Tellina rastellum</i> Hanley 1844	R	—		
<i>Tellina robusta</i> Hanley 1844	R	—		
<i>Tellina tenuilirata</i> Sowerby 1867	O	2d,9	MS	IX
<i>Tellina rosamunda</i> Melvill & Standen 1907	R	9	S	IX
<i>Tellina wallaceae</i> Salisbury 1934	F	8,9	S	I,XII
<i>Exotica clathrata</i> Deshayes 1854	R	9	S	XII
<i>Macoma edentula</i> (Spengler 1798)	KR	9	S	XII
<i>Apolymetis coarctata</i> (Philippi 1845)	R	—		
<i>Tellinides emarginata</i> (Sowerby 1825)	KR	—		
<i>Tellidora pellyana</i> H. Adams 1873	O	—		



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Species	Localities		Months found	
Donacidae				
<i>Donax clathratus</i> Deshayes 1854	O	—		
<i>Donax cuneatus</i> Linnaeus 1758	R	—		
<i>Donax scalpellum</i> Gray 1857	C	—		
Psammobiidae				
<i>Gari maculosa</i> (Lamarck 1818)	R	—		
<i>Gari occidens</i> (Gmelin 1791)	O	—		
<i>Gari violacea</i> Recluz	C	—		
<i>Gari weinkauffi</i> (Crosse, 1864)	R	4	S	II
<i>Psammotella ruppelliana</i> Reeve 1857	O	—		
<i>Asaphis deflorata</i> (Linnaeus 1758)	R	2b,5	S	II
Semelidae				
<i>Semele sinensis</i> Reeve 1850	R	3,9	S	L,XII
<i>Semele scabra</i> Hanley 1845	R	—		
<i>Abra cadabra</i> Eames & Wilkins 1957	KF	—		
Solecurtidae				
<i>Solecurtus quoyi</i> Sowerby 1854	KR	—		
<i>Solecurtus australis</i> (Dunker 1861)	R	—		
Trapeziidae				
<i>Trapezium sublaevigatum</i> (Lamarck 1819)	O	2a,3,6	H	I,II,VI
Veneridae				
<i>Callista lilacina</i> Lamarck 1818	F	4,6,7	S	I,II
<i>Lioconcha picta</i> (Lamarck 1818)	R	—		
<i>Circe corrugata</i> (Dillwyn 1817)	O	8,11	SM	IV,VI,VII
<i>Circe scripta</i> (Linnaeus 1758)	F	2d,6,8,11	SM	III,VI,IX,XI
<i>Circenita callipyga</i> (Born 1778)	C	2a,3,5,6,8,11	SM	II,VI,XI
<i>Dosinia alta</i> (Dunker 1848)	O	6	S	II
<i>Dosinia exoleta</i> (Linnaeus 1758)	R	6	S	II,XII
<i>Dosinia hepatica</i> (Lamarck 1818)	F	5,8	S	I,XII
<i>Bassina callophyla</i> (Philippi 1836)	R	—		
<i>Gafrarium pectinatum</i> (Linnaeus 1758)	R	3	+	IV
<i>Irus irus</i> (Linnaeus 1758)	C	3,5,6	+H	II,VII,VIII,XI
<i>Periglypta puerpera</i> (Linnaeus 1771)	R	—		
<i>Marcia cor</i> (Sowerby 1853)	KF	2d,2e	M	II,IX
<i>Marcia hiantina</i> (Lamarck 1818)	C	2a,2c,8,11	MS	I,II,IV
<i>Marcia opima</i> (Gmelin 1791)	O	11	M	II
<i>Meretrix meretrix</i> (Linnaeus 1758)	C	2a,2c,11	M	II,XII
<i>Paphia gallus</i> (Gmelin 1791)	O	5,9	S	XII
<i>Paphia sulcaria</i> (Lamarck 1818)	C	2a,8	S	II
<i>Sunetta effossa</i> Hanley 1842	R	—		
<i>Tapes textile</i> (Gmelin 1791)	R	—		
<i>Timoclea arakana</i> (G. & H. Nevill 1871)	KR	2d	S	IX
<i>Timoclea farsiana</i> Biggs 1973	F	2d,4	S	I,IX
<i>Timoclea macfadyeni</i> Dance & Eames 1966	F	—		
<i>Venerupis deshayesei</i> (Hanley 1852)	R	3	S	II
<i>Clementia papyracea</i> (Gray 1825)	R	—		
Petricolidae				
<i>Petricola hemprichi</i> Issel 1869	O	3,6	H	I–XII
<i>Claudi concha corrugata</i> (Gmelin 1791)	O	5	H	VII
Myidae				
<i>Tugonia divaricata</i> (Reeve 1863)	R	—		



Species	Localities	Months found
<b>Corbulidae</b>		
<i>Corbula sulculosa</i> A. Adams 1870	O 4	H II
<i>Corbula modesta</i> Hinds 1843	R —	
<i>Corbula modesta acuminata</i> Hinds 1843	R 5	H II
<b>Gastrochaenidae</b>		
<i>Gastrochaena cuneiformis</i> Spengler 1783	O 5,8	H I—XII
<b>Pholadidae</b>		
<i>Aspidopholas obtecta</i> (Sowerby 1848)	C 16(6)	+ II
<i>Pholadidea striata</i> (Linnaeus 1758)	F 5,6	H I—XII
<i>Martesia</i> sp. K1450	R 12b	H XI
<b>Teredinae</b>		
<i>Teredo</i> sp K1421	KO 16(6)	+ II
<b>Laternulidae</b>		
<i>Laternula</i> n.sp. K1421	R 5	+ II
<i>Laternula anatina</i> (Linnaeus 1758)	R —	
<b>Cephalopoda</b>		
<b>Sepiidae</b>		
<i>Sepiella inermis</i> Ferussac & d'Orbigny 1835	C —	

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# LANDSNAILS FROM SOUTHERN LEBANON

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*Abstract:* 22 species are reported from southern Lebanon. The malacofauna of southern Lebanon is very similar to that of northern Lebanon, and of northern Israel. In most species the largest specimens are from an altitude of 400 m. Apparently this altitude contains the optimal conditions, in terms of mild mediterranean climate, for the development of large snails.

## INTRODUCTION

Very little is known about the malacofauna of southern Lebanon, of the area extending some 60–80 km ( $\times$  50 km) south of Beirut towards the northern border of Israel. This paucity of knowledge is somewhat odd, since we have a very reasonable knowledge as to the landsnails of neighbouring regions,—of northern Lebanon, of south-western Syria and of Israel (Germain 1921, Pallary 1929, 1939, Haas 1951, 1955, Heller 1971, 1974, 1975, Mienis 1982 and many other papers, Forcart 1976 and many others). Southern Lebanon, in the midst of these ‘well-grazed’ regions, has remained practically unexplored but for a few isolated sites along its coast (e.g. Nordsieck 1971).

In December 1982–January 1983 I spent 30 days in southern Lebanon, and during this period I was able to collect some landsnails. Collecting was opportunistic rather than systematic, and was frequently carried out under unfavourable conditions of pressure in time and physical risk. This present collection should therefore be regarded as no more than a dash at the malacofauna of southern Lebanon, in an attempt to gain some basic impression as to its faunal diversity and relationships; it is not an extensive, detailed work. For each species I give merely the sites at which it was found, and one or two measurements (for *Pene*, in which the taxonomy is rather difficult, I give further measurements). The material is preserved in the mollusc collection of the Hebrew University, Jerusalem.

## RESULTS

### Prosobranchia

#### Pomatiasidae

*Pomatias olivieri* (de Charpentier 1847). Damur (4 shells); shell-height  $20.0 \pm 0.1$  mm. Barja (2 shells); shell-height  $17.2 \pm 0.1$  mm. Sidon-Jezzin road, above the Awwalli River (1 shell); shell-height 17.6 mm. Nabbattiya (3 shells); shell-height  $23.6 \pm 0.1$  mm. *P. olivieri* is a dweller of calcareous soils in humid climates, usually on slopes facing the sea. It spends most of its time buried in the soil, of a depth of 5–10 cm.

### Pulmonata

#### Chondrinidae

*Rupestrella rhodia* (Roth 1839). Barja (2 shells); these were not measured to avoid damaging

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Fig. 1. Map of southern Lebanon, with localities mentioned in this text.

their fragile shells. This species is a rock-dweller that inhabits the under sides of stones and rocks.

#### Enidae

*Buliminus labrosus* (Olivier 1804). Barja (10 shells); shell-height  $29.1 \pm 1.3$  mm. Sidon-Jezzin road, above the Awalli River (5 shells); shell-height  $33.5 \pm 1.2$  mm. These Lebanese samples are similar in size and shell proportions to *labrosus* of northern Israel (Heller 1975), and thus belong to the nominate subspecies *l. labrosus*.

*Pene syriacus* (Pfeiffer 1846). Jezzin, 2 km north of (4 shells); shell-height  $17.5 \pm 0.5$  mm, shell-diam  $5.6 \pm 0.3$  mm, mouth-height  $5.7 \pm 0.3$  mm, mouth diam  $4.3 \pm 0.1$  mm. The taxonomy and distribution of *P. syriacus* has been described elsewhere (Heller 1974). The sample from Jezzin differs from *syriacus ramimensis* of Israel in the more roundish mouth, in the peristome that is reflected sideways rather than forwards, and in the bluish, rather than brown colour of most of the shells.

*Pene sidoniensis* (de Férussac 1821). Gebel Tsaffi, 5 km south of Jezzin (2 shells); shell-height  $13.8 \pm 10.9$  mm, shell-diam  $4.8 \pm 0.7$  mm, mouth-height  $4.8 \pm 0.7$  mm, mouth diam  $3.3 \pm 0.7$  mm. The detailed taxonomy and distribution of this species has been described elsewhere (Heller 1974).



*Pene* cf. *auriculata* (Pallary 1929). Rashaya el-Wadi (2 shells); shell-height  $17.5 \pm 0.9$  mm, shell-diam  $5.8 \pm 0.2$  mm, mouth height  $5.7 \pm 0.2$  mm, mouth-diam  $4.0 \pm 0.3$  mm. The shells from southern Lebanon are somewhat intermediate, in their proportions, between *P. auriculata* of Israel and *P. syriacus* of north-eastern Lebanon (as given by Heller 1974). Only further samples can verify the precise taxonomic status of these shells, and of the *auriculata-syriacus* relationship in general.

*Paramastus episomus* (Bourguignat 1857). Damur (2 shells); shell-height  $14.4 \pm 0.6$  mm. Nabbattiya (2 shells); shell-height  $20.1 \pm 1.8$  mm. The systematic position and distribution of this species has been described elsewhere (Heller 1971). *P. episomus* tends to bury itself in the ground in rocky, limestone habitats.

*Euchondrus septemdentatus* (Roth 1839). Damur (16 shells); shell-height  $8.1 \pm 0.5$  mm. Jezzin, 2 km north of (1 shell); shell-height 10.3 mm. Nabbattiya (15 shells); shell-height  $10.3 \pm 0.6$  mm. This species is a typical rock-dweller, frequently found on the undersides of stones.

### Clausiliidae

*Cristataria strangulata* (Pfeiffer 1841). Damur (6 shells); shell-height  $15.1 \pm 1.2$  mm. The detailed taxonomy and distribution of the genus *Cristataria* is described by Nordsieck (1971). This species was found mainly on vertical rocks and cliffs.

*Elia moesta* (Rossmässler 1839). Damur (10 shells); shell-height  $12.5 \pm 1.2$  mm. *E. moesta* differs from *C. strangulata* with which it is sympatric, in that it is found usually on the ground beneath stones, rather than on vertical surfaces.

### Zonitidae

*Eopolita protensa* (de Férussac 1832). Barja (1 shell); shell-diam 8.3 mm. Jezzin, 2 km north of (1 shell); shell-diam 12.1 mm. This carnivorous species is the most common zonitid in the mediterranean landscapes of Israel.

### Limacidae

*Deroceras* sp. Nabbattiya (1 live specimen); this specimen was neither measured, nor preserved.

### Sphincterochilidae

*Sphincterochila cariosa* (Olivier 1804). Nabbattiya (12 shells); shell-diam  $15.8 \pm 0.7$  mm. *S. cariosa* is widely distributed in mediterranean landscapes in Israel in the mountain region, where it frequently buries itself in the soil.

### Helicellidae

*Xeropicta vestalis* (Pfeiffer 1848). Jezzin, 2 km north of (7 shells); shell-diam  $10.0 \pm 0.2$  mm. Nabbattiya (25 shells); shell-diam  $14.6 \pm 0.2$  mm. Jezzin (8 shells); shell-diam  $9.9 \pm 0.2$  mm. In view of the recent studies on shell polymorphism in *Xeropicta vestalis* from Israel (Heller & Volokita 1981, 1982), it would be interesting to examine the extent of shell darkness in the Lebanese populations. Using the same scoring methods as those used by Heller & Volokita, the results are: Jezzin, 7.2; Jezzin, 2 km north, 8.9; Nabbattiya, 9.1. The Lebanese populations are thus considerably paler than those of the Judean Hills, where the pigmentation index is 21–26 (Heller & Volokita 1981). Apparently the Lebanese climate forces the snails into a life cycle that is quite different from that which prevails in the mediterranean habits of central Israel.

*Monacha haifaensis* (Pallary 1939). Damur (1 shell); shell-diam 8.8 mm. Barja (5 shells); shell-diam  $8.7 \pm 0.5$  mm. Jezzin (5 shells); shell-diam  $9.7 \pm 1.0$  mm. Nabbattiya (11 shells); shell-diam  $8.6 \pm 0.8$  mm. All these shells are smaller than those recorded by Heller &



Tchernov (1978) from Israel: in the coastal plain of Israel the diameter of *M. haifaensis* averages 10.6 mm, and in the hilly region it averages 11.7 mm. This species is, in general, a plant-dweller that is found mainly upon the stems of the vegetation.

*Monacha crispulata* (Mousson 1861). Damur (3 shells). The shells were not measured, so as not to damage their delicate hairs. In Israel, this species is found uncommonly in humid, often moldy biotopes beneath stones.

*Metafruticicola fourousi* (Bourguignat 1863). Sidon-Jezzin road, above the Awwalli River (1 shell); shell-diam 16.8 mm. *M. fourousi* is an uncommon landsnail in mountain mediterranean landscapes.

## Helicidae

*Theba pisana* (Muller 1774). Tyre (30 shells, collected in an orchard and nearby field); shell-diam  $15.7 \pm 1.7$  mm. The Lebanese population is similar in size to the populations of the southern coast of Israel (Heller, 1982). Morph frequencies: 1234—3%; 0234—33%; 0034—13%; 0000—50%; These frequencies offer further evidence that the 'effectively banded' shells (a category which includes the morphs 1234 and 0234) are not more common in the northern parts of *T. pisana*'s range in the Levant (where it is more cool and humid than in more southern parts), as has been suggested by Nevo & Bar (1976). The sample from Tyre falls well within the pattern of frequencies suggested by Heller (1981).

*Eobania vermiculata* (Muller 1774). Damur (2 shells); shell-diam  $29.5 \pm 3.1$  mm. Tyre (4 shells); shell-diam  $27.0 \pm 0.9$  mm.

*Levantina caesareana* (Mousson 1854). Damur (2 shells); shell-diam  $33.0 \pm 0.3$  mm. Barja (3 shells); shell-diam  $33.7 \pm 1.1$  mm. Nabbattiya (13 shells); shell-diam  $34.3 \pm 2.3$  mm. Hatsbaya, 6 km north of (8 shells); shell-diam  $32.7 \pm 1.2$  mm. The detailed distribution in Israel of this obligatory rock-dwelling helcid has recently been described by Heller (1979).

*Helix aspersa* Müller 1774. Damur (7 shells); shell-diam  $34.7 \pm 1.2$  mm.

*Helix engaddensis* Bourguignat 1852. Barja (3 shells); shell-diam  $26.8 \pm 1.9$  mm. Mt. Tsaffi, 5 km south of Jezzin (2 shells); shell-diam  $25.3 \pm 2.4$  mm. Nabbattiya (3 shells); shell-diam  $32.1 \pm 2.0$  mm. Hatsbaya, 6 km north of (2 shells); shell-diam  $27.0 \pm 1.1$  mm. *H. engaddensis* is widely distributed in Israel, not only in mediterranean but also in arid biotopes.

## DISCUSSION

All the 22 species here reported from southern Lebanon have previously been described from more northern parts of Lebanon (Germain 1921, Pallary 1929, 1939). Nineteen of them have also been found further south, in the mediterranean parts of Israel. This present paper thus serves to emphasize the fact that Lebanon and Israel form one single, continuous malacological unit, with a very similar fauna.

Three southern-Lebanese species, *Cristataria strangulata*, *Eobania vermiculata* and *Helix aspersa*, are not found in Israel. *C. strangulata* is replaced, in Israel, by members of the morphologically very close *C. genezarethana* species-group. *E. vermiculata* and *H. aspersa* are found in Israel only in some urban gardens, as introduced populations (Mienis 1973). The area around Damur (where they were found in a natural biotope) probably represents the southernmost natural range of these mediterranean species in the Levant.

Many species from the mediterranean parts of Israel have not yet been recorded from southern Lebanon. One such group of species includes *Pilorcula raymondi*, *Truncatellina haasi*, *Ena benjamitica*, *Granopupa granum*, *Punctum lederi*, *Vitrea contracta*, *Calaxis* spp. and *Ceciloides acicula*. All these species are of small size, have a disjunct, very localized distribution, and are largely subterranean; with patient collecting many of them may, eventually, be found also in southern Lebanon. Another group of mediterranean species found in Israel but not in



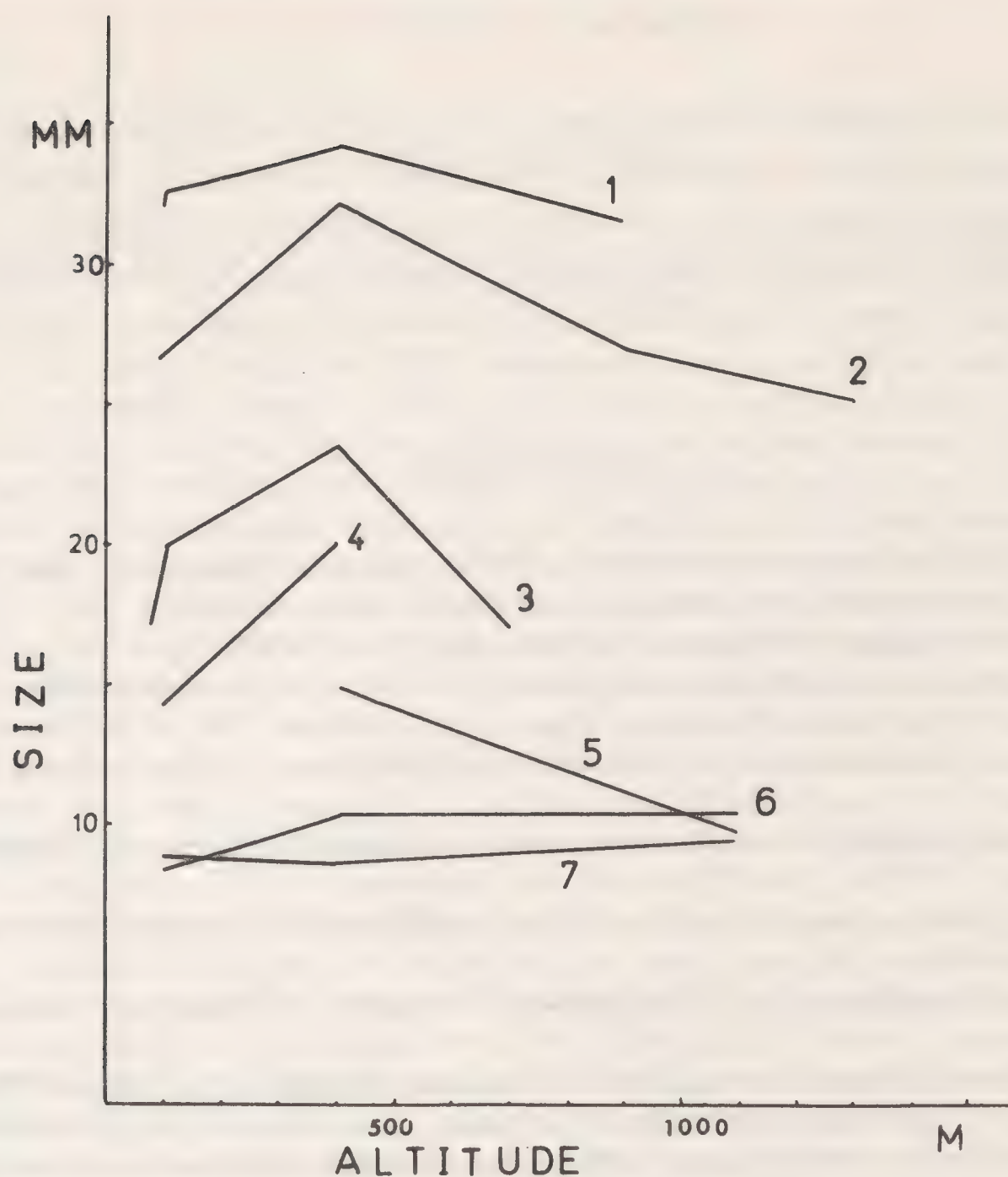


Fig. 2. Relation between shell size and altitude, in landsnails from southern Lebanon: 1—*Levantina caesareana*; 2—*Helia engaddensis*; 3—*Pomatias olivieri*; 4—*Paramastus episomus*; 5—*Xeropicta vestalis*; 6—*Euchondrus septemdentatus*; 7—*Monacha haifaensis*.

southern Lebanon includes *Euchondrus ovularis*, *E. sulcidens*, *Cernuella arrouxi*, *Caracollina lenticula*, *Trochoidea davidiana* and *T. picardi*. These species are, in general, dwellers of stabilized sand-dunes and of calcareous sandstone—habitats that are scarce in southern Lebanon, so that their absence from this present collection probably reflects a certain reality.

Upon examining intraspecific variation in the southern Lebanese fauna, a common trend can be noted: in the majority of species, snails from the montane hinterland are of considerably larger shell-size than those from the hills overlooking the coast (Barja, Damur). This is somewhat odd, for the coast is more humid, in summer, than the mountains further to the east. The association with altitude is not a linear one: as Fig. 2 shows, most species reach their maximum size at the altitude of 400 m; beyond this altitude, shell-size tends to decrease. Apparently this altitude contains the optimal conditions, in terms of mild mediterranean climate, for the development of large snails. Only a much more detailed collecting of snails, and a more thorough knowledge of climatic and edaphic data, will enable a better understanding of the biological significance of this conchiological trend.



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## REVIEWS

*Die Landschnecken Nord- und Mitteleuropas*. By M. P. Kerney, R. A. D. Cameron & J. H. Jungbluth. Verlag Paul Parey, Hamburg/Berlin, 384 pp., 24 colour plates, numerous text-figures, 368 distribution maps. DM 58.—ISBN 3-490-17918-8.

Kerney & Cameron's excellent field guide (1979) has been widely used on the continent. Foreign editions seemed to be a matter of time and market. Already in 1980 Dr E. Gittenberger's Dutch version was published, which also proved to be a success among a section of the western European malacological community. The Dutch book exhibits some additional features, viz., a well illustrated chapter on the snails of the mediterranean parts of France (specially composed by Kerney for this edition) and a nine page key by Gittenberger. The distribution maps of the British Isles were not incorporated. Dr. J. H. Jungbluth is responsible for the German adaptation (1983) of the field guide, which so far is undoubtedly the best available. It is also the bulkiest and, with a price of between £14 and £15, certainly the most expensive version. In the reviewer's opinion it is definitely worth it. The original work has 288 closely printed pages, Gittenberger's edition contains 310 less closely printed pages, and the German version numbers no less than 384 closely printed pages.

What does make the German book so valuable? First of all, it covers a much larger area than the two earlier editions. The land snails of Austria, Hungary, Czechoslovakia and Poland have been incorporated throughout the text, i.e. either as species not treated in the earlier editions or in the form of additional distribution data. Secondly, this has necessitated the addition of 92 line drawings of prime quality. Finally, the French mediterranean chapter by Kerney of the Dutch edition is also included. The result of the above alterations/additions is that the European distribution maps (a total of 368 against 276 in the original book) have all been emended or newly supplied; moreover, a really contrasting colour has been used this time, adding to the value of the maps.

Gordon Riley's colour plates are as good as ever. The additional line drawings have been made by two staff artists of the Rijksmuseum van Natuurlijke Historie, Leiden, Ms. Inge van Noortwijk and Wim Gertenaar. This has been done under the supervision of the curator of molluscs of the Leiden museum, Dr E. Gittenberger, who has also supplied a lot of new data. The new figures may be recognized by the fact that the inside of the aperture usually is uniformly black (see e.g. on pp. 126–127, the figures of *Vallonia alamannica* are new). The work of these highly skilled professional artists is both aesthetically pleasing and functional. It is therefore to be regretted that on p. 71 the right-hand figure of *Acicula callostoma* has been reversed; this regularly, but fortunately rarely, occurs in the malacological literature, and represents the kind of gastropod to be eradicated.

Unfortunately Gittenberger's concise but valuable key has been replaced by a selection of the most common types of shells and slugs depicted on the end-papers, so that the families may be recognized. However, the beginner's best bet is assiduously to page through the figures and plates in order to identify his specimens with some confidence. Other innovations are German common names for many species (should not everyone rather start by memorizing the scientific names which normally are or should be universally applicable?) and a glossary of technical terms. The reviewer was very pleased to see the recommended comma inserted between the name of the author and the year of description of the scientific name. This is unusual for a German author and, indeed, most commendable.

There are no local German distribution maps; the book has been written for a German readership which covers at least four nations.

With every foreign edition Kerney & Cameron is getting bigger and better; however, we should never forget that the real pioneering work was done by the people who created the book in the first place. Of course, taxonomic opinions are bound to change at times in details and not everybody will agree with the decisions taken. Nevertheless, Jungbluth's version of Kerney & Cameron is now the best and most complete book available to anyone working with or interested in western, northern and central European land snails. Even if you do not read German, you should buy it for its illustrations and distribution maps. The reviewer considers this book one of the best available in its field.

A. C. VAN BRUGGEN

*Natural History Manuscript Resources in the British Isles*. By G. D. R. Bridson, V. C. Phillips, and A. P. Harvey, xxxiv+473pp, Mansell, London: R. R. Bowker & Co., New York, 1980. Price £97.00.

The bane of any historian using primary sources is the finding, or in many cases, not finding relevant archival material. Until now his success in the natural history field has relied on a happy combination of expertise, familiarity with existing catalogues of individual depositories and sheer luck. The work in question aims to reduce the tedious task of fruitless enquiries by attempting to catalogue, in one volume, all natural history manuscripts in the British Isles.

The authors have used a laudably wide and flexible definition of manuscript to include such diverse material as



annotated copies of printed works, manuscript copies of the original pattern sets, correspondence, bills, inventories etc. The inclusion of photocopies of manuscripts is however perhaps a little too catholic an interpretation.

To make the project feasible, only depositories in the British Isles are surveyed. Unfortunately, this therefore includes, by definition, not only material concerned with foreign natural history, but also excludes material on British natural history housed in foreign depositories. The scope of the book is further limited by the omission of some important depositories, i.e. those in private hands (presumably because of problems of access and security) and the Public Record Office (presumably because of the sheer weight and diversity of its contents as well as the existence of a printed catalogue).

The archives of some of the larger provincial museums appear to have been excluded. I would hope that this is unintentional because these must, at the very least, contain material relevant to the institutions themselves and to the local natural history societies. Although these omissions may be the result of the disruptive effect of local government re-organisation, which interrupted the survey, I suspect that it owes much to local authority centralisation of archival responsibility into one department, so that museum archives are ignored as being extra-departmental or incorporated without separate identification. The result is anything if not confusing, but hardly the fault of the authors.

It is difficult to identify the exclusion of individual manuscript collections because by their very nature, they may have never been previously catalogued. Omissions may be attributable to the method of the book's compilation, i.e. the supplementation of data gleaned from existing catalogues by a questionnaire followed by a personal visit. Although a valuable tool, the questionnaire inevitably brings into question the validity of the results, i.e. its accuracy, completeness, extent and uniformity of coverage. Inevitably the entries are the result of subjective judgements not only by those compiling the original catalogues, but also by those completing the questionnaires and those editing the results. It is hoped that some uniformity if not objectivity was introduced by the personal visit, but physical endurance alone must have precluded detailed visits to all 443 depositories listed.

Turning to the book itself, I found it particularly easy to use. The initial pages of introduction by D. E. Allen (who is credited as being one of the main inspirers of the work) and the authors' explanatory preface is followed by an annotated general bibliography, the brevity of which (7 pages) belies its considerable usefulness as an introduction for the novice and a checklist for the more experienced worker. The main body of the text, 379 pages, is arranged alphabetically in order of place names. The individual institutions have an address, telephone number, hours of opening, together with details of any catalogues, printed or otherwise, and whether the archives are recorded at all by the National Register of Archives. The archives themselves are separated into collections which are individually identified by a unique sequential number, prefixed by that of the institution. This decimal notation is used throughout for indexing. The collections are so arranged that those relating to the institution and to local societies have precedence and are followed by correspondence (under the collector's name) etc. in alphabetical order. Each collection is briefly described as to its size and contents.

In general, the animal kingdom is the best represented by extant archives, with the plant kingdom coming a close second; molluscs being more fully treated than any other invertebrate group except the insects. The poor coverage of the fossil mollusca, despite the enormous number of extinct species reflects the general sparse earth science coverage. The general impression after consulting all the archives indexed under Mollusca was that the collections referred predominantly either to the published works of Lister, da Costa and the Sowerby's or to local collections of mollusca. Archives on the mollusca are widely scattered and it comes as no surprise to find that the most extensive molluscan archival collections are primarily in the National Museums.

The indexing, which to my mind, is a general indicator of a book's scholastic value, is particularly detailed and occupies almost one fifth of the book. It is divided into three sections, i.e. names, places and subjects, which index not only the collection heading but also the individual items it contains. The subject index utilises a hierarchical decimal system to enable detailed cross-referencing, so that, for instance, molluscan collection can be located under collection—mollusca or Mollusca—collection. The Mollusca can in fact appear in four sections—namely collections (22 items), drawings (31 items), living fauna (148 items) and fossil (16 items). Although some of the divisions are contrived (would one in fact really wish to look at just drawings of molluscs without looking through the entire molluscan entry?) and there is ample scope for duplication e.g. drawings of a fossil molluscan collection, there is less than would be anticipated. The system works well.

The index has been compiled, and must therefore be used, intelligently. The words 'shell' and 'conchology', although appearing in the text, are included in the index only as 'mollusca'.

My initial attitude to this book's publication was ambiguous; while obviously welcoming anything which more fully documented primary sources, I was at the same time perturbed that such a wealth of information so readily available would remove, so to speak the 'excitement of the chase', the unexpected discovery of an essential manuscript. This was but wishful thinking. This book but catalogues collections and only sparingly describes their significant contents. Such an appraisal is at best subjective and cannot hope to identify items of significance to a particular researcher. In any event while there are still entries such as 'Hoyle W. E. 2 boxes of assorted material unsorted' (National Museum of Wales) and 'William Swainson miscellaneous manuscripts unsorted' (Cambridge), there is obviously scope for further work which without this publication might remain unknown to those interested.



## REVIEWS

This book attempts therefore to bring together the natural history researcher and the relevant manuscripts. The need for a comprehensive catalogue of natural history archives has long existed and the present work goes a long way to satisfying it. It is disappointing that the book's prohibitive price will inevitably restrict the number of purchasers to a minute fraction of those who will undoubtedly consult it.

PETER F. LINGWOOD



## COMMUNICATIONS

### VERTIGO ANGUSTIOR LIVING NEAR ITS TYPE LOCALITY IN SOUTH WALES

*Vertigo angustior* Jeffreys is a rare snail found in wet permanently marshy grassland allegedly or amongst moss in damp hollows in sand-dunes. Although there are many dead-shell records of unknown age from flood debris, the species has recently been recorded living only at three sites in Britain: (1) Flordon Common, Norfolk (*J. Conch., Lond.* **28** (1974), pp. 141–154); (2) Martlesham Creek, East Suffolk (*J. Conch., Lond.* **31** (1983), p. 257); and (3) Gait Burrows National Nature Reserve, N. Lancashire (*J. Conch., Lond.* **31** (1983), p. 72). The last site was ecologically anomalous in that the species was found in mossy hollows within limestone pavement. In Ireland it is more common and is known from several sites on the west coast.

Jeffreys originally described *V. angustior* in 1830 from shells found 'Among the rejectamenta of a small stream at Marino near Swansea' (*Trans. Linn. Soc. Lond.* **16**, p. 362). Although Jeffreys subsequently listed additional localities for *V. angustior* including Tenby (*British Conchology* **1** (1862), p. 266), Marino was the only site given with the original description and this must therefore be regarded as the type locality. No-one has succeeded in finding living specimens at either of these Welsh sites or anywhere else in western Britain and these records have usually been dismissed as fossils.

In 1924 Dr H. E. Quick discovered 'remarkably fresh' shells of *V. angustior* in shell pockets within the dune complex at Oxwich Bay, Gower, just 10 km. S.W. of Marino (*J. Conch., Lond.* **17** (1924), p. 223). Despite prolonged searching in the area during the following years (*J. Conch., Lond.* **18** (1926), pp. 57; (1927), 119–122), Quick failed to find living specimens. In May 1983 we succeeded in finding this elusive colony at Oxwich as well as a further site on the north coast of Gower.

The habitat at Oxwich Bay (SS511877) was an area of open marshy ground lying between the dune complex and the saltmarsh further west. Strands of flood debris (chiefly dead *Juncus*) indicated that much of the area was submerged during high water spring tides. The characteristic vegetation here was composed of *Senecio aquaticus* Hill, *Juncus maritimus* Lam., *Mentha aquatica* L., *Bidens tripartita* L., *Potentilla anserina* L., *Iris pseudacorus* L., *Cratoneuron filicinum* (Hedw.) Spruce. The associated Mollusca were *Carychium minimum*, *Cochlicopa lubrica*, *Columella edentula*, *Vallonia pulchella*, *Punctum pygmaeum*, *Arion ater*, *A. intermedius*, *Nesovitrea hammonis*, *Deroceras reticulatum*, *D. laeve*, *Euconulus fulvus*, *Clausilia bidentata*, *Trichia hispida*, *Cepaea nemoralis*.

The habitat of the second site, Whitford Burrows, extended for about 2 km. (SS451958–SS439939) and was broadly similar. *V. angustior* occurred only at the transition between dune and saltmarsh. This zone varied between 15–30 m. in width and lay about 10 m. above the strand-line. The vegetation here, which was heavily grazed by horses, consisted chiefly of *Mentha aquatica* L., *Potentilla anserina* L., *Hydrocotyle vulgaris* L., *Iris pseudacorus* L., *Oenanthe cf. crocata* L., *Juncus acutus* L., *Cratoneuron filicinum* (Hedw.) Spruce and *Calliargon cuspidatum* (Hedw.) Kindb. Associated Mollusca were *Carychium minimum*, *Cochlicopa lubrica*, *Columella edentula*, *Vertigo substriata*, *Vallonia pulchella*, *Arion ater*, *A. intermedius*, *Nesovitrea hammonis*, *Deroceras reticulatum*, *D. laeve*, *Trichia hispida*, *Cepaea nemoralis*.

One particularly obvious feature at both sites was that *V. angustior* never occurred in direct association with *V. antivertigo*, although the two could be found within a metre of each other. The latter species always occurred in wetter conditions. This observation is in complete accord with their antipathetic behaviour during the early Postglacial (e.g. *Phil. Trans. R. Soc. Lond. B* **291** (1980), pp. 1–43). The disappearance of *V. angustior* from many inland sites may be linked with the spread of forest during the Postglacial, although man has undoubtedly contributed by draining large areas of wetland. The survival of *V. angustior* in coastal areas in western Britain may possibly result from the fact that these were never completely forested during the Postglacial. The survival of *V. angustior* in abundance in such sites in Gower demonstrates that further attention should be paid to similar sites elsewhere in western Britain and Ireland.

We thank Mr M. Hughes and Mr M. Davies, the wardens of Oxwich and Whitford Burrows respectively, for help and Dr D. T. Holyoak for identifying the plants.

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### ASHFORDIA GRANULATA AND PONENTINA SUBVIRESCENS IN N. BRITTANY

*Ashfordia granulata* (Alder) was first described from Stella and Walbottle Deans in north-east England (Alder, *Trans. nat. Hist. Soc. Northumbl.* **1** (1830), p. 39). Elsewhere in Britain it has a wide but patchy distribution extending from Scotland, Ireland and England to the Scilly Isles and even the Channel Isles (Kerney (1976), *Atlas of the non-marine Mollusca of the British Isles*).



## COMMUNICATIONS

On the continent its occurrence has long been disputed and several authors (e.g. Jaeckel (1962), *Die Tierwelt Mitteleuropas* **2** (1), *Ergänzungen*) list it as exclusively British. However there are two fairly reliable continental records. The first is from Morlaix, Finistère, where it was recorded by Bourguignat in 1860 (*Malacologie terrestre et fluviatile de la Bretagne*) as *Helix psaturochoeta* from under stones near the hospital wall as far as 'le ruisseau du Relec'. Germain (*Arch. Mus. Hist. nat. Lyon* **13** (1929), pp. 1–484) subsequently accepted the identity of this species with *A. granulata*. The second record is from the north coast of Spain and is based on eight shells in the R. Macandrew Collection at the University Museum of Zoology, Cambridge, originally labelled '*Helix Serica* Müll Gijon RM' (*Arch. Molluskenk.* **107** (1976), pp. 111–114).

During a visit to the north coast of Brittany in May 1983 several further localities for *A. granulata* were discovered where it was abundant. These were (a) Trégastel (UTM 10 km sq VV 60) in gardens and hedges; (b) Port Blanc (VV 70) climbing walls near the sea front; and (c) Ile de Bréhat (WV 01) under stones and rubbish. These sites are approximately 50 km east of Morlaix and *A. granulata* will doubtless prove to be equally common at other sites along the Côtes-du-Nord and northern Finistère.

*Ponentina subvirescens* lives in grassland close to the sea and has been found in several coastal areas of western France including southern Brittany (Kerney & Cameron (1979) *A Field Guide to the Land Snails of Britain and North-west Europe*). Its occurrence near Port Hir (VV 81) on the Côtes-du-Nord apparently constitutes its first record from north Brittany although it does occur in the Channel Isles.

R. C. PREECE

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# ONTOGENETIC CHANGE OF SHELL COLOUR PATTERNS IN *LITTORINA NEGLECTA* BEAN (1844)

CELIA J. HANNAFORD ELLIS\*

(Accepted for publication, 15 October 1983)

**Abstract:** The shells of *L. neglecta* are usually patterned with bands, tessellations or a mixture of both. These have been considered to be genetically different colour morphs (Anderson 1974). Here it is shown that the pattern type changes with age, younger animals typically have banded shells and in older ones they are tessellated.

## INTRODUCTION

*Littorina neglecta* Bean (1844) is aptly named. A tiny species, rarely growing larger than 4 mm, it is usually found at low tide inside the shells of dead barnacles. It is therefore comparatively unobtrusive and is a less familiar species than its larger, widely-researched and controversial relative *L. saxatilis* (Olivi 1792). Aspects of the biology of this latter species has been the subject of nearly thirty papers, whereas *L. neglecta* has been considered in only five since Heller redescribed the species in 1975. Raffaelli (1978) studied the effect on *L. neglecta* population density and size structure, of changes in the availability and size of the small crevices formed by dead barnacles and the spaces between barnacles. Sneli & van Marion (1979) reported on its occurrence and habitat at two fjords in Norway. Wilkins & O'Regan (1980) noted differences in the allele frequencies at gene loci encoding phosphoglucose isomerase and phosphoglucomutase in *Littorina* species and in both *L. neglecta* and *L. saxatilis* found an unexpectedly high level of heterozygosity. Fretter (1980) discussed the comparative anatomy of the female littorinid genital duct including *L. neglecta*. Hannaford Ellis (1983) suggested that the species is an annual.

The barnacle belt of British rocky shores might be described as a wrinkle nursery ground, juveniles of all the wrinkle species cohabit with *L. neglecta* and those of the other rough wrinkle species are especially common. The majority of *L. neglecta* shells are distinctively patterned (Heller 1975) and so can be easily identified. In Anglesey the pattern is of tessellations or bands of pigment, varying in shade from yellowish brown to chestnut on a pale background colour, white, biscuit and fawn shades are usual. A consistent feature of patterned shells is a wide band (Fig. 1, w-band) which runs into the aperture of the shell. However at all the sites from which I have collected *L. neglecta* there are some shells that are unpatterned, and are either pale or completely dark brown. The identification of these is a little more difficult, but with practise they can be recognised on a combination of shell shape, quality and sub-opercular pattern (Hannaford Ellis 1980) and it is not usually necessary to examine the soft parts.

The occurrence of plain and patterned shells may be a polymorphism, but has yet to be critically studied. However the different types of patterning, tessellations, bands or mixed bands and tessellations have been considered to be polymorphisms by Anderson (1974). He proposed that apostasy and environmental diversity were involved in the maintenance of the polymorphism. He also demonstrated a significant negative correlation between the striped

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morph of *L. neglecta* and the lined morph of *L. nigrolineata*. However, the examination of the ontogeny of the shell pattern made here, suggests that the nature of the pattern is a function of age rather than a polymorphism.

## METHODS

Large collections of *L. neglecta* were made at two sites in Anglesey, Porth Swtan (Grid reference SH299892) on the 7th July 1977 and Porth Diana (Grid reference SH253784) on the 17th July 1978. At each site collections were made starting at a point and radiating out from it, collecting all the small winkles as systematically as possible. The samples were sorted for *L. neglecta* and the shell heights were measured under a binocular microscope fitted with an eyepiece graticule. The shell colours were noted and the patterned shells were scored into the following classes of pattern (see Fig. 1):—

Class 1: completely banded

Class 2: mixed tessellations and bands (excluding the w-band)

Class 3: completely tessellated (excluding the w-band)

## RESULTS

The total sample sizes were 390 animals from Porth Swtan and 231 from Porth Diana. Some of these were unpatterned (see Table 1) and completely dark shells were twice as common as completely light shells. Unpatterned shells were four times commoner at Porth Diana.

TABLE 1

Disposition of shell colouring at the two sites.

	Porth Swtan	Porth Diana
Patterned shelled	375	192
Pale shelled	5	13
Dark shelled	10	26
% of pale and dark shelled in sample.	4%	17%

For the patterned shells the percentage of each pattern class in successive 0.25 mm size groups were calculated and plotted (Fig. 2). The data from both sites show an obvious association between the type of patterning and shell height: Small shells are nearly all banded and large shells are nearly all tessellated. The change in pattern takes place at a smaller size at Porth Swtan than at Porth Diana. Thus at Porth Swtan about 65% of *L. neglecta* in size group 4 (1.75–1.99 mm) will have class 2 shell patterns compared to about 50% at Porth Diana. Also larger sized animals are more frequent at Porth Diana and the largest measured 3.4 mm. The largest animal from Porth Swtan was 2.6 mm.



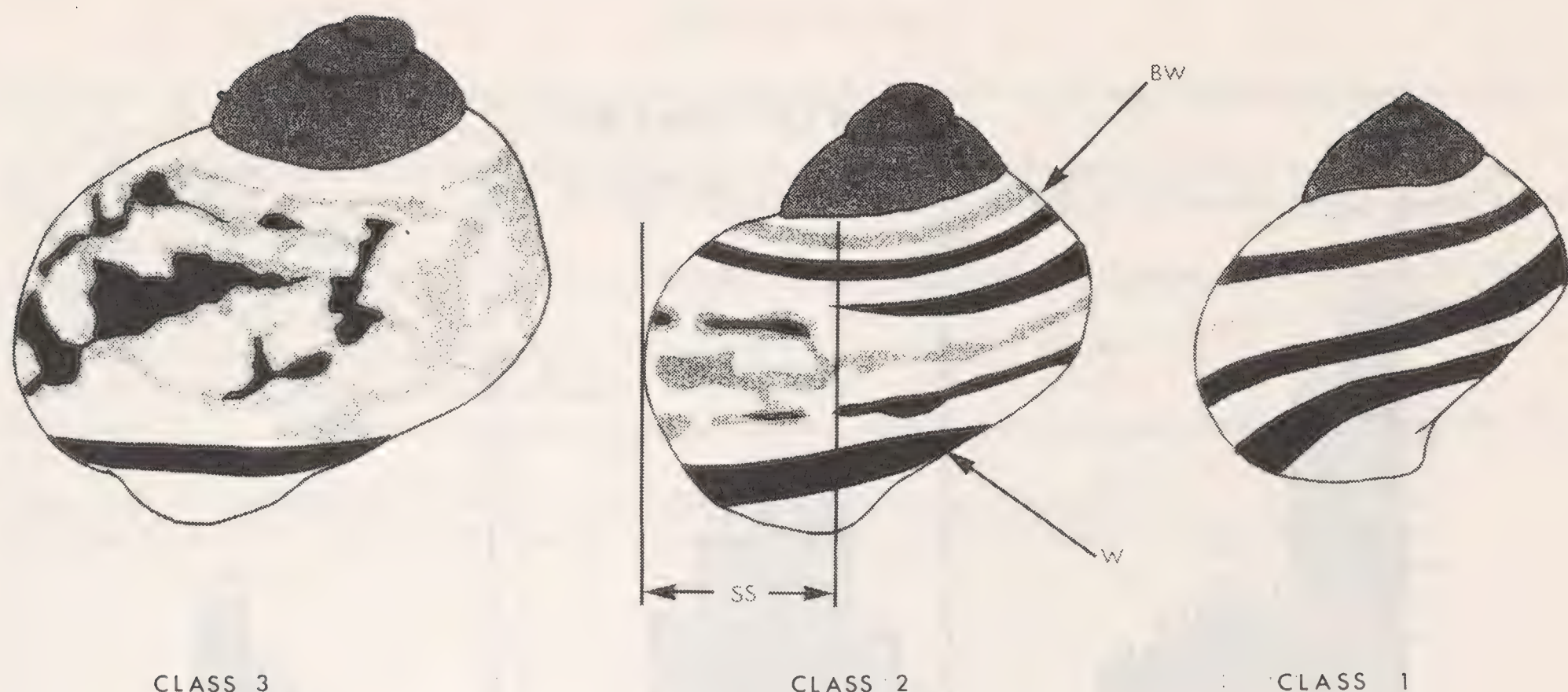


Fig. 1. Colour pattern classes: BW – body whorl, SS – scored section of body whorl, W – w-band.

### DISCUSSION

The results indicate that there is an ontogenetic change in patterning. This is supported by the observation that in tessellated shells the older part of the shell, (where it is not eroded or overlain) is banded, whilst the reverse situation has not been seen. Clearly banded and tessellated “morphs” cannot be regarded as genetically distinct as suggested by Anderson (1974).

It is interesting to speculate on why this change in pattern should occur. Whilst patterning seems subjectively cryptic, this does not explain why patterning changes with an apparently minor increase in size. The physiological effects of shell colour may be the underlying cause: dark shells absorb heat more effectively than light shells, with concomitant implications for rates of growth, feeding, breeding etc. Bands and tessellations could provide a mechanism for fine tuning of the heat absorbancy of a shell relative to animal volume, and the proportion of dark coloration could be sensitively tuned to precise local conditions either phenotypically or, in view of the ovoviviparity and consequent low dispersion rates of the species, genetically. Indeed the difference in size frequency distributions at the two sites points to local influences affecting the populations.

The maintenance of the uniformly dark and light shells in the population probably has a different explanation and Anderson (1974) has suggested that frequency-dependent predation is responsible. Another possibility is that heterozygous advantage might be the underlying cause.

However the negative correlation of striped *L. neglecta* with lined *L. nigrolineata*, noted by Anderson must be regarded as spurious. Marked changes over a year in the size structure and sexual development of the *L. neglecta* population at Porth Swtan indicates that it is an annual species (Hannaford Ellis 1983). Thus the percentage of striped-shelled animals in the population will be correlated to the season in which they are examined.

### ACKNOWLEDGEMENTS

I am grateful to Professor A. J. Cain for his help during the course of this study and to Mr



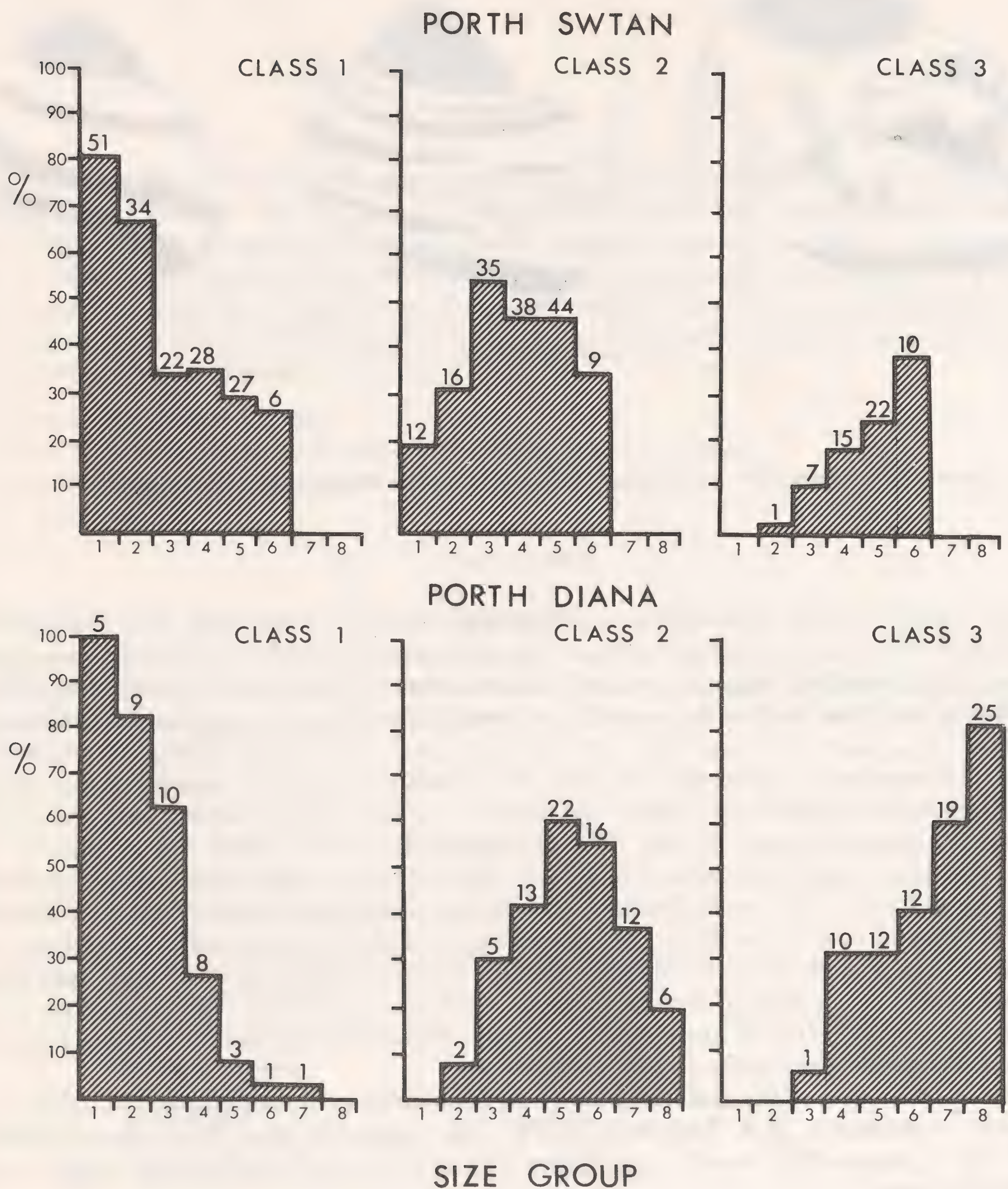


Fig. 2. Histograms of percentage in pattern class, (the number in the sample is shown above each bar). Size groups: 1, 1.00–1.24 mm; 2, 1.25–1.49 mm; 3, 1.50–1.74 mm; 4, 1.75–1.99 mm; 5, 2.00–2.24 mm; 6, 2.25–2.49 mm; 7, 2.50–2.74 mm; 8,  $\geq 2.75$  mm.

A. de C. Baker for his constructive comments on an earlier draft of this paper. The project was undertaken during the tenure of a research studentship from NERC.



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## OBITUARY

### *Arthur Peter Hoblyn Oliver, 1918–1984*

Peter Oliver died suddenly on Friday, 6th April 1984. He was 65. Born in Sandown, Isle of Wight, he was educated at Uppingham School and on leaving in 1936 he joined the Asiatic Petroleum Co. In 1940 he married Mary Carrington and in the same year enlisted in the London-Scottish Territorials and was shortly afterwards transferred to the Seaforth Highlanders with the rank of Lieutenant. During the retreat to Dunkerque in 1940 he was captured at St. Valary and remained a p.o.w. in Germany until his release in 1945. During his long captivity Peter became an expert bridge player and was a formidable opponent in this game of skill.

After his discharge from the army in 1946 Peter attended the London School of Oriental Languages and was then sent by his employers to China where he remained for three years. After this he was transferred to Africa, serving in the Sudan, Kenya and on the west coast. In 1960 he returned to the Far East as a P.R.O. for the Shell Oil Co. working in Singapore and Malaya where he became a founder member of the local malacological society and first started to collect marine shells. He finally returned to England in 1966 and worked at the Shell Centre in London until his retirement.

It was a source of considerable regret to Peter that he did not take up shell collecting until his return to the Far East in 1960 and that he had missed wonderful opportunities to do so, in east and west Africa. However, he succeeded in making a very extensive collection just the same. He was particularly interested in the Cypraeidae, Volutidae and Conidae making himself a recognized authority on the latter. His collection was a general one, although confined to marine gastropods. The considerable number of marine bivalves he collected in Malaya and Singapore still remain unworked at his death.

He was a fellow of the Linnean and Zoological Societies of London and an active member of the Conchological Society of Great Britain and Ireland and had served on the Societies' Council on numerous occasions. He was also a member of the Hawaiian Malacological Society and the British Shell Collectors Club of which he was a past president.

Peter will be best remembered for his one major publication, *The Hamlyn Guide to Shells of the World*, Hamlyn, London 1975, illustrated by the late James Nicholls. This popular guide became a conchological best seller. It was translated into a number of languages. There is also an American edition.

Those who wanted shells identified or were just after advice always found a warm welcome at his beautiful country home at Crowhurst in East Sussex, where he was always ready to make his magnificent collection available to all who cared to call. His untimely passing will leave a gap amongst conchologists that will be hard to fill.

T. PAIN



# *CUTHONA GENOVAE* (O'DONOGHUE 1926), AN AEOLID NUDIBRANCH NEW TO THE FAUNA OF THE BRITISH ISLES

B. E. PICTON\* and K. WILSON†

(Accepted for publication, 18 February 1984)

*Abstract:* *Cuthona genovae*, a common Mediterranean nudibranch, is recorded for the first time outside the Mediterranean from Lough Hyne, Co Cork, Ireland. It is described and figured and compared with its close relative *Cuthona foliata* (Forbes & Goodsir 1839). The previously known distributions of these two species suggested that *C. genovae* replaced *C. foliata* in the Mediterranean. The records given here show that they are in fact sympatric over a considerable part of their ranges, and confirm their distinct specific status.

## INTRODUCTION

As part of an investigation of the nudibranch fauna of Ireland Lough Hyne was visited by the authors on several occasions in 1980. Two nudibranchs with Mediterranean/warm temperate Atlantic distributions were found there for the first time in the British Isles in August 1980; *Facelina dubia* Pruvot-Fol 1948 and *Dicata odhneri* Schmekel 1967. (Picton & Brown 1981). The discovery of a population of *Cuthona genovae* in the lough suggests that S.W. Ireland may harbour other species presently known only from the Mediterranean.

## MATERIAL

Amongst hydroids and Ascidians, underside of fishing vessel, N.W. Quay, Lough Hyne, Co Cork, Ireland 51° 30.2' N 9° 18.5' W. Three specimens Coll. B. E. Picton and K. Wilson 14.12.1980. Ulster Museum catalogue. No. Mn 5202.

Amongst tubes of the polychaete *Serpula vermicularis*, the Salt Lake, Clifden, Co Galway, Ireland. 53° 28.5' N 10° 01.0' W. One specimen. Coll. C. A. Maggs and D. W. McGrath. 8.12.1981. Ulster Museum catalogue No. Mn 6194.

## DESCRIPTION

This is the smallest *Cuthona* species in the British Isles, mature animals measuring between 4 mm and 6 mm. The pigmentation of the head, oral tentacles, rhinophores, and fore part of the body is complex. The distal two thirds of the oral tentacles and rhinophores are yellow, with translucent tips and a sub-apical orange band, which is broad on the oral tentacles but narrow on the rhinophores. The basal third of the oral tentacles is translucent. The basal quarter of the rhinophores is covered with white pigment, separated from the yellow region by a translucent band. White pigment forms patches on the dorsal surface of the head and pericardium, and streaks and patches on the sides of the head. There is a

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† K. Wilson Department of Zoology, University College, Cork.



pattern of scarlet pigment on the head and body consisting of a crescent shaped mark behind the pericardium, a patch on each side in front of the first ceratal bases, a similar patch on each side just behind the oral tentacles, a third pair of marks on each side just below the rhinophores, and a transverse line across the front of the head. There is a stripe of lemon yellow along the centre of the head, between the rhinophores. Further patches of white pigment occur down the midline of the back, and on the sides of the body between the ceratal groups.

The cerata are short and squat, and are arranged in a pre-anal group of 3 rows and 3 or 4 post-anal rows. Each row consists of 3 or 4 cerata. The surface of a large ceras is covered with gold dust-like pigment interspersed with clear patches through which the dark green digestive gland can be seen. The apex of the ceras is clear, followed by a ring of white pigment and a ring of orange pigment. In one small specimen this second ring of pigment was missing, leaving a clear region. The orange bands on the rhinophores and oral tentacles were also absent in this specimen.

The radula of a 5 mm specimen consists of 59 rows of teeth, with 5 or 6 denticles on each side of the median cusp. The anterior reproductive complex was dissected out and mounted after staining and clearing. It is fairly typical for a *Cuthona*, including a bursa, a short prostatic vas deferens, a large sac-like penial gland, and a hooked chitinous penial stylet.

#### DISCUSSION

Bouchet (1976) has shown that although *C. genovae* and *C. foliata* have been confused by many authors in the past, they are actually quite distinct in details of their colour pattern and anatomy. No other European *Cuthona* species has a similar pattern of red markings on the head and back. *C. genovae* has a lemon yellow stripe down the centreline of the head, absent from *C. foliata*. (See Fig. 1).

The extension of the known range of *C. genovae* from the Mediterranean to S.W. Ireland indicates that it is not confined to the Mediterranean, replacing *C. foliata* there, as suggested by Bouchet (1976), but actually has a distribution which overlaps with that of *C. foliata* on the Atlantic coast of Europe. This provides proof that these two forms are full species rather than geographically isolated subspecies and supports Bouchet's treatment of them.

Lough Hyne has been shown to contain a number of species of nudibranch previously only known to occur much further to the south (Wilson and Picton 1983). The significant find of *C. genovae* in Co Galway as well as in Lough Hyne suggests that an investigation of similar habitats elsewhere on the west coasts of Ireland might result in the discovery of further populations of such species. These sites may be characterised by becoming significantly warmer than offshore water during the summer – Lough Hyne typically reaches 17°–20° as opposed to 13°–15° C offshore.

#### ACKNOWLEDGEMENTS

We would like to thank Christine Maggs for diving support at Lough Hyne in December 1980 and Christine Maggs and Dave McGrath for collecting the specimen from Galway and providing us with information about it. We also thank Gillian Sands for preparing the drawings.



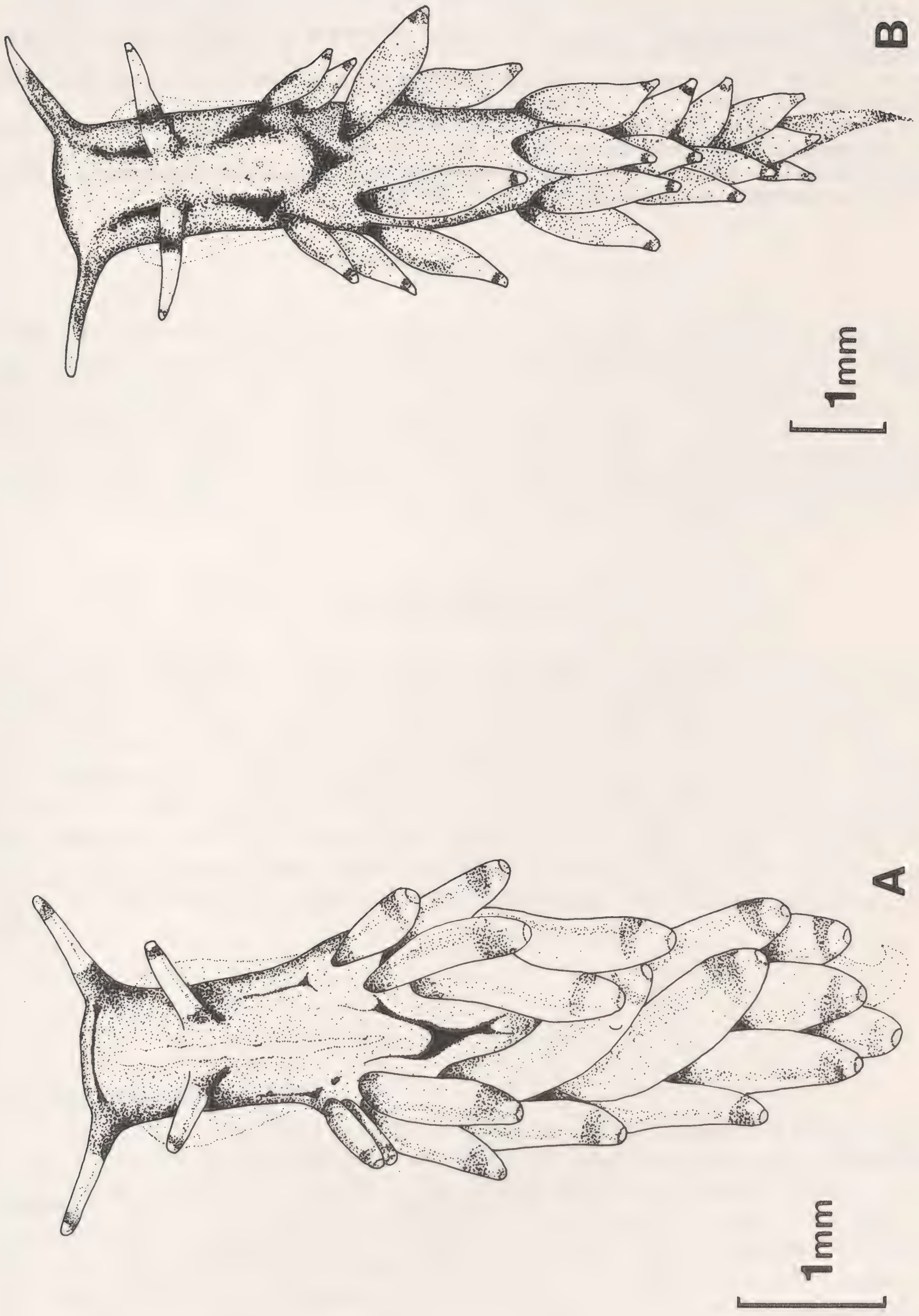


Fig. 1. A. *Cuthona genovae*, B. *Cuthona foliata*, dorsal views.



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# ON THE IDENTITY OF *CONUS ANAGLYPTICUS*, *CONUS BACCATUS*, *CONUS SELENAE* AND *CONUS* *YEMANJAE*

DANKER L. N. VINK\*

(Accepted for publication, 18 February 1984)

*Abstract:* *Conus anaglypticus* Crosse, occurring along the northern coast of Puerto Rico, is a valid species distinct from *Conus mindanus* Hwass in Bruguière. It can be distinguished from *Conus selenae* Van Mol, Tursch & Kempf by the rather sharp shoulder of the body whorl and the smooth tops of the spire whorls. *Conus baccatus* Sowerby III is only known from the holotype, which shows similarities with certain specimens of *C. selenae*, but cannot be identified unequivocally with that species. If further collections would confirm conspecificity, *C. selenae* must be considered a junior synonym of *C. baccatus*. *Conus selenae* Van Mol, Tursch & Kempf is tentatively maintained as a valid species occurring along the northern and northeastern coast of Brazil. *Conus yemanjae* Van Mol, Tursch & Kempf is a form of *C. selenae* with large granules on the shoulder of the body whorl and on the margin of some earlier whorls.

## INTRODUCTION

The taxonomy of the genus *Conus* is far from being settled. In a number of cases, even with the type material available for study, it is not yet possible to identify unequivocally the species in nature that the author intended to denote by his specific name. With more field work in recent years the situation has greatly improved but still many problems exist. In this study two enigmatic species will be discussed of which the type material is present in British museums, i.e. *Conus anaglypticus* Crosse, and *Conus baccatus* Sowerby III. Both species have a small, pustulose shell with a convex body whorl, and both species show similarity with the more recently described *Conus selenae* Van Mol, Tursch & Kempf and *Conus yemanjae* Van Mol, Tursch & Kempf. In view of this similarity these latter nominal species will also be dealt with.

## REVIEW OF SPECIES

### *Conus anaglypticus* Crosse 1865

Crosse (1865, Pl. 11, Fig. 8 and 8a) described and figured two varieties of *Conus anaglypticus*. The two specimens figured, together with a third specimen from the type lot which must be considered a syntype are present in the British Museum (Natural History), London (1979183/1,-/2,-/3). The specimen (1979183/1) illustrated by Crosse (1865, Fig. 8) was figured by Coomans, Moolenbeek & Wils (1980, p. 48, Fig. 86) as holotype. This specimen (Pl. 20, Fig. 8) is a small shell (17.3 mm) with a convex body whorl and a rather high, straight spire. The body whorl is covered with regularly disposed spiral rows of small granulations. Although Crosse described the colour as uniform orange to pale red, there is also a mid-body band of indistinct somewhat darker squares. Similar dark reddish squares alternated with white maculations are present on the spire whorls. The specimen 1979183/3 shown in Crosse

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(1865, Fig. 8a) as 'variété  $\beta$ ' is somewhat smaller (16.0 mm) with a more reddish colour. It has obsolete spiral ridges on the lower part of the body whorl but is not granulated. Crosse indicated the Antilles as habitat.

Tomlin (1937) synonymized *C. anaglypticus* with *C. mindanus* Bruguière, Clench (1942) placed the species in synonymy with *C. verrucosus* Hwass, while Abbott (1958) considered both *C. anaglypticus* and *C. verrucosus* referable to *C. jaspideus* Gmelin. Subsequently Wagner & Abbott (1967) and Van Mol, Tursch & Kempf (1967) placed *C. anaglypticus* in synonymy with *C. jaspideus*. Tucker (1977), however, made the observation that the smooth and orange-white embryonic whorls of *C. anaglypticus* as described by Crosse, are 'not usual for *C. jaspideus*'. He erroneously identified *C. anaglypticus* with an Indo-Pacific species, based on Crosse's Fig. 8, which he thought showed an 'orange shell with black pustules'. Walls (1979) synonymized *C. anaglypticus* again with *C. mindanus*, and Coomans, Moolenbeek & Wils (1980) also concluded that the specimen of *C. anaglypticus* shown in Crosse (1865, Fig. 8) 'represents a juvenile of the granulated form of *C. mindanus*'.

Cone shells closely resembling the type material of *C. anaglypticus* are found off the northern coast of Puerto Rico at depths of 10 to 20 m. Six specimens from this population were available for study (17.4 to 11.6 mm). Four of these specimens (e.g. Pl. 20, Fig. 9) show the same convex body whorl, the same straight spire, the same rows of small granulations and the same orange to pale red coloration as the specimen shown in Crosse (1865, Fig. 8) (in one of these specimens there is a distinct lighter coloured band below the mid-section). Two other specimens with weak granulation (e.g. Pl. 20, Fig. 10) resemble the 'variété  $\beta$ '. In these specimens the mid-body band of darker squares is more pronounced and the dark patches are alternated with white maculations, furthermore white axial flames are present.

It is obvious that *C. anaglypticus* from Puerto Rico should not be referred to *C. jaspideus*. In my opinion this population should also be excluded from the *C. mindanus* complex. Subspecies and forms belonging to the species complex of *C. mindanus* (e.g. Pl. 20, Fig. 7) have the tops of the spire whorls distinctly concave and not nearly flat as in *C. anaglypticus*. Furthermore the body whorl is always less convex, and the granulations in pustulose specimens are larger. In the Western Atlantic only *C. selenae* Van Mol, Tursch & Kempf could be confused with *C. anaglypticus*, this species is discussed below.

#### *Conus baccatus* Sowerby III 1877

Sowerby (1877, Pl. 75, Fig. 5) described and figured *C. baccatus*. The holotype is present in the National Museum of Wales (34.01.29) and was figured by Coomans, Moolenbeek & Wils (1982, p. 54, Fig. 197). This specimen (Pl. 20, Fig. 1) is a small shell (22.2 mm) with a convex body whorl, a broad shoulder, a rather short spire and spiral rows of widely spaced granules. The colour is whitish with orange blotches arranged in 3 spiral bands. In particular near the base orange dashes can be observed between the granules. Sowerby made the observation that the shell 'is remarkable for the double angle at the top of the body-whorl'. The type locality is unknown.

Since its description no further specimens of *C. baccatus* have been recorded. Tomlin (1937) simply listed the species, Wagner & Abbott (1967) indicated 'No information', Walls (1979) suggested to refer *C. baccatus* to *C. mindanus* (Pl. 20, Fig. 7), but Coomans, Moolenbeek & Wils (1982) rightly pointed out that 'there is no relation to *C. mindanus* Hwass, 1792'. They provisionally considered *C. baccatus* a valid species but made the observation that 'the holotype might be a juvenile shell of an earlier described species'.

Studying colour photographs of the holotype I saw similarities between *C. baccatus* and *C. yemanjae* as pictured by Van Mol, Tursch & Kempf (1967, Pl. 8, Fig. 1a), a small, broadly shouldered cone shell with spiral rows of widely spaced granules. The possible relationship is discussed below.



*Conus selenae* Van Mol, Tursch & Kempf 1967

Van Mol, Tursch & Kempf (1967, Pl. 8, Fig. 2a, 2b, 2c) figured *C. selenae* and described the species from northern and northeastern Brazil. The holotype is present in the Muséum National d'Histoire Naturelle, Paris, one paratype has been deposited in the Museum of Comparative Zoology, Cambridge, Mass. (registered number 278239). The holotype is a small shell (14 mm) with a convex body whorl sculptured with spiral rows of widely spaced granulations which are aligned in such a way that axial plicae are formed. However, in this species the sculpture is most variable and entirely smooth shells are also found. The colour is whitish with violet to orange brown blotches arranged in 2 irregular spiral bands. Typical *C. selenae* has 2 to 3 distinct spiral ridges with low granules on the spire whorls.

*Conus yemanjae* Van Mol, Tursch & Kempf 1967

Van Mol, Tursch & Kempf (1967, Pl. 8, Fig. 1a, 1b) figured and described *C. yemanjae* from 2 specimens, one shell dredged off the state of Sergipe, Brazil and another shell recovered ex-pisce at Fortaleza. The first specimen has been deposited as holotype in the Muséum National d'Histoire Naturelle, Paris. This specimen (12 mm) resembles *C. selenae* but is more broadly shouldered and has larger granules interconnected by brown dashes. There are no distinct spiral ridges on the tops of the spire whorls, but 2 zones can be distinguished separated by a groove. Large granules are present on the shoulder of the body whorl and the margin of some earlier whorls.

## COMPARISON OF SPECIES

For further investigation of the possible relationship of the above nominal species 15 specimens of *C. selenae* and *C. yemanjae* from various localities along the Brazilian coast were compared. Sculpture and colour of these specimens varied widely, 7 shells corresponded rather well with the typical form of *C. selenae* (Pl. 20, Fig. 4), 3 shells had the triangular shape and granulated shoulder of *C. yemanjae* (Pl. 20, Fig. 3), 2 shells were entirely smooth (Pl. 20, Fig. 2) and 3 specimens were smooth but worn shells. In the granulated specimens the granulation could be heavy or indistinct, the granules could form axial plicae or a cobblestone texture, and be close set or widely spaced. The background colour could be white, pinkish or yellow; the maculations reddish, orange or brown.

One of the 3 specimens with the triangular shape of *C. yemanjae* (Pl. 20, Fig. 5) had granules aligned in plicae and spiral ridges on the earlier whorls as in *C. selenae*, some specimens of the 7 more typical *C. selenae* had the more triangular shape of *C. yemanjae*. There is no predominance of one of the two nominal species in a particular area. After carefully studying the material available I agree with Abbott (1974), Walls (1979), Kempf (personal communication 1980) and Tursch (personal communication) that *C. yemanjae* cannot be considered a valid species, the status of a form seems to be correct. As regards distribution of the various forms of *C. selenae* is concerned, study of the material confirmed the observation by Kempf (personal communication) that a predominance of larger, smooth specimens can be observed near the North West part of the range (states of Maranhao and Pará), where specimens are found in deeper waters with more muddy bottom. As mentioned above *C. anaglypticus* could be confused with *C. selenae* (Pl. 20, Fig. 6), it has the same convex body whorl and rather high straight spire as the more typical specimens of *C. selenae*. However, the tops of the whorls are smooth, without spiral ridges as in typical *C. selenae*. It is true that distinct spiral ridges may be absent in smooth forms of *C. selenae* but in these specimens 1 or 2 faint spiral cords can be observed. Furthermore *C. anaglypticus* differs from these forms by showing a rather sharp angle at the shoulder of the body whorl. In my opinion *C. anaglypticus* from more northern waters should be maintained as a valid species.



Comparing the holotype of *C. baccatus* with the available specimens of *C. selenae*, the similarity in colour pattern with one specimen of the smooth form (Pl. 20, Fig. 2) is striking. In both specimens the orange brown maculations are well delimited at the side near the lip but gradually fading away at the opposite side. In both specimens spiral lines of brown dashes can be observed, and both specimens show a double angle at the top of the body whorl. Close inspection of the 'smooth' specimen showed that very weak widely spaced spiral ridges are present on the body whorl. These ridges are more apparent in one specimen of the form *C. yemanjae* (Pl. 20, Fig. 3) with widely spaced granules. Both the holotype of *C. baccatus* and this specimen of *C. yemanjae* are not just pustulate shells, but, in the words of Sowerby characterised by 'rows of gem-like granules' (hence the name, '*Conus baccatus*', the cone adorned with pearls). The holotype of *C. baccatus* has a shorter spire and relatively smaller nuclear whorls, but these differences can be attributed to the larger size of this specimen; in fact it is larger than any of the specimens of *C. selenae* s.l. studied.

From the above it could be concluded that the characteristics of the holotype of *C. baccatus* (except the size) fall within the variability of characters observed in *C. selenae*, and that *C. baccatus* should be considered conspecific with this species (in which case *C. baccatus* is the nominee). However, the type of *C. baccatus* cannot be considered an intergrade between the smooth form from the North West part of the range and *C. yemanjae* with widely spaced granules from the North East part, which is always smaller and more stocky. It rather looks like another granulated form of the smooth specimens of *C. selenae* from deeper and more muddy water off Maranhao and Pará, but such specimens have not been collected as yet in recent times. Although there are strong indications that *C. baccatus* and *C. selenae* are synonymous, a firm conclusion can only be drawn once more material has become available.

#### ACKNOWLEDGEMENTS

I am grateful to Dr. M. Kempf (Centre océanologique de Bretagne, Brest), Dr. B. M. Tursch (Université Libre, Brussels) and Mr. C. J. Finlay from Florida for the loan of specimens, and to Mrs. K. M. Way (British Museum (Natural History), London) for permitting me to study the type specimens of *Conus anaglypticus*. I wish to thank Dr. P. G. Oliver (National Museum of Wales, Cardiff) for the photographs of the holotype of *Conus baccatus*.

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VINK: *CONUS*

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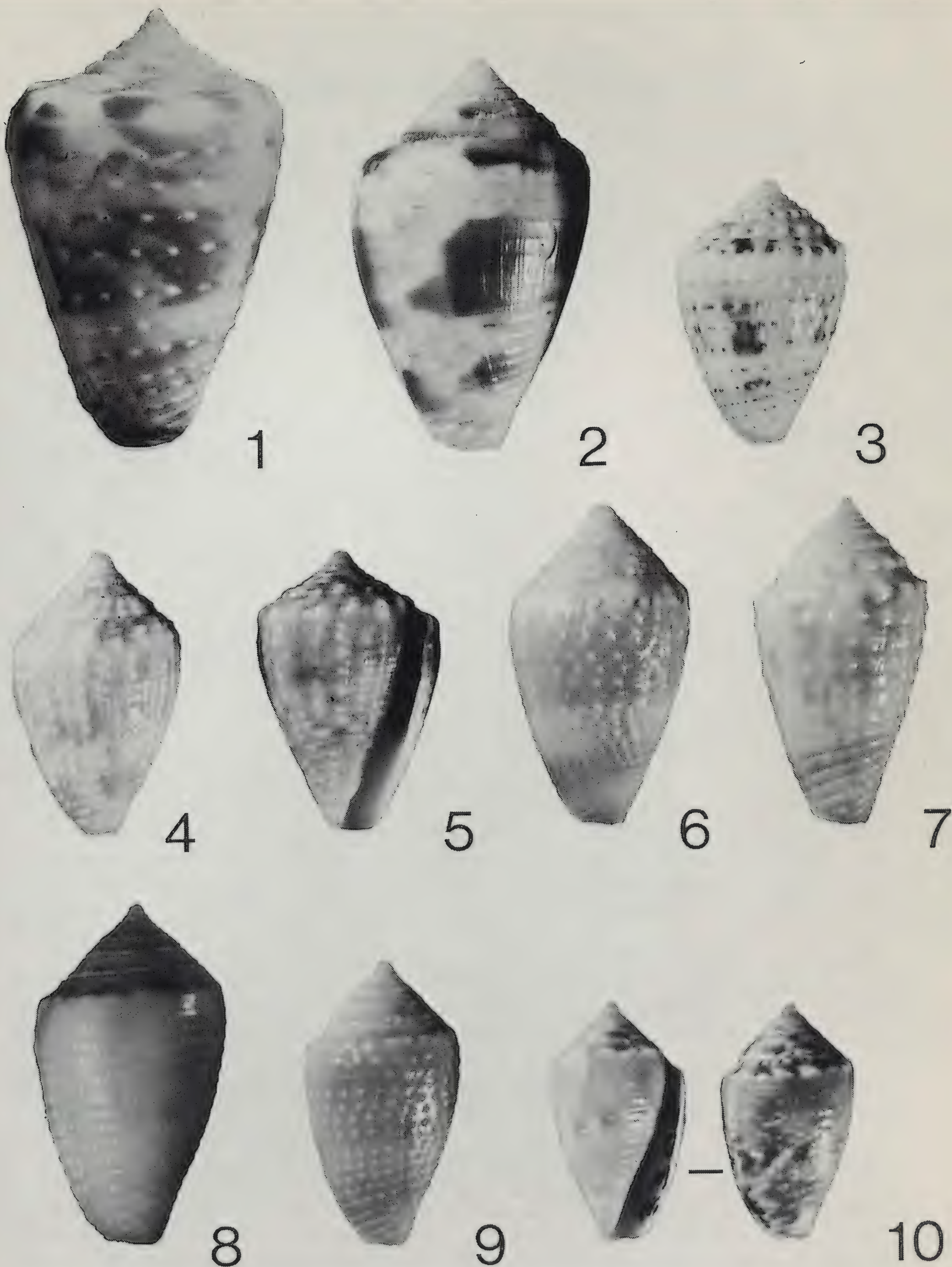


PLATE 20

Scale: approx.  $2\frac{1}{2}\times$  natural size

- Fig. 1. *C. baccatus*, holotype, ex Melvill-Tomlin collection, National Museum of Wales, Cardiff, no. 34.01.29. Photograph courtesy National Museum of Wales (height 22.2 mm).
- Fig. 2. *C. selenae*, between São Luis and Parnaíba (State of Maranhão), Brazil, 65 m muddy sand bottom, Kempf collection. Smooth specimen with a colour pattern resembling that of the holotype of *C. baccatus* (height 19.9 mm).
- Fig. 3. *C. selenae*, Fortaleza (State of Ceará), Brazil, 70 m calcareous algae bottom, Kempf collection. Specimen with widely spaced granules closely resembling the holotype of *C. yemanjáe*, a form of *C. selenae* (height 13.3 mm).
- Fig. 4. *C. selenae*, State of Ceará, Brazil, Tursch collection. Specimen closely resembling the holotype of *C. selenae* (height 14.2 mm).
- Fig. 5. *C. selenae*, State of Pará, Brazil, 70 m, Kempf collection. Specimen with granulated shoulder like *C. yemanjáe*, but with granules aligned in plicae as in *C. selenae* (height 14.2 mm).
- Fig. 6. *C. selenae*, Maceio (State of Alagoas), Brazil, 36 m calcareous algae bottom, Vink collection. Specimen somewhat resembling *C. anaglypticus*, but with rounded shoulder of the body whorl (height 16.3 mm).
- Fig. 7. *C. mindanus*, Hollywood (Florida), USA, 15 m sand and rubble bottom, Vink collection. Pustulose specimen somewhat resembling *C. anaglypticus*, but with concave tops of the spire whorls, less convex body whorl and larger pustules (height 16.5 mm).
- Fig. 8. *C. anaglypticus*, specimen figured in Crosse (1865, Fig. 8) ex Cuming collection, British Museum (Natural History), London no. 1979183/1 (height 17.3 mm).
- Fig. 9. *C. anaglypticus*, between San Juan and Loíza Aldea, Puerto Rico, beach specimen, Vink collection. Specimen closely resembling the specimen shown in Fig. 8 (height 14.4 mm).
- Fig. 10. *C. anaglypticus*, Puerto del Tortuguero, Puerto Rico, 10 m coral biotope, Vink collection. Less pustulose specimen somewhat resembling the specimen figured in Crosse (1865, Fig. 8a) as *C. anaglypticus* 'variété  $\beta$ ' (height 11.9 mm).











# THE ADAPTATIONS OF *FRENAMYA CEYLANICA* (BIVALVIA: ANOMALODESMATA: PANDORACEA) TO LIFE ON THE SURFACE OF SOFT MUDS

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**Abstract:** A representative of the Anomalodesmata—*Frenamya ceylanica* (Pandoracea: Pandoridae)—from Hong Kong is described. Details of the ligament confirm that *Frenamya*, hitherto considered but a subgenus of *Pandora*, is a valid genus and is re-established. *Frenamya* is either slightly buried or lives on the surface of soft sublittoral muds. In various ways, including a deeply recessed mantle margin, powerful cleansing currents in the mantle cavity, copious mucus production and long proximal oral grooves, *Frenamya* is adapted to high amounts of sediment in suspension and the consequent removal of large quantities of pseudofaeces from the mantle cavity. *Frenamya* shows convergent similarities with the discoidal *Placuna placenta* (Anomiacea: Placunidae) to life on such substrates, i.e. extreme lateral compression and a form that enables both to 'float' on the mud surface. *Frenamya* is not discoidal but a greatly expanded posterior shell face, gives a broad scimitar shape, that fulfils the same function. In both, a sunken, dorso-ventrally elongate, primary ligament and long 'secondary' hinge teeth or crura, serve to prevent shear and align the shell valves. A dorsal 'secondary ligament' of fused periostracum assists in valve alignment and prevents sediment gaining access to the dorsal region of the shell. *Frenamya* occupies a habitat essentially similar to that of *Placuna* but has a narrower range because of the restrictions imposed by simultaneous hermaphroditism and, probably, as in *Pandora*, a short larval life. The reproductively simpler *Placuna* is more widely dominant on such substrates in the tropics.

## INTRODUCTION

The Anomalodesmata is one of the least studied and most diverse sub-classes of the Bivalvia. It has recently been reviewed by Morton (1981). Each species occupies a highly specialised niche so that they are both rare and their adaptations exotic. They include, for example, the predatory septibranchs (Reid and Reid 1974) and the watering-pot shells, e.g. *Clavagella* and *Brechites* (Morton 1984a, b).

There are few records of anomalodesmatans from the South China Sea. From Hong Kong only two have hitherto been reported upon: both belong to the Laternulidae—*Laternula truncata* from the seaward fringe of mangrove muds and *L. anatina* in offshore (7–8 m) deposits (Morton 1976). During a trawling programme in Mirs Bay, a specimen of *Frenamya ceylanica* was obtained from offshore muds at a depth of 8–10 m.

No representative of the family, except *Pandora* (Allen 1954, Boss & Merrill 1965), has been examined anatomically. Accordingly, the specimen of *Frenamya* has been dissected and sectioned and is here reported upon.

Pelseneer (1911) gave a brief description of *Pandora elongata*. Boss and Merrill (1965) have reviewed that Atlantic Pandoridae and given a description of *P. gouldiana*. Habe (1952, 1977) has reviewed the Japanese species, but *F. ceylanica* does not occur in either list. Allen (1954) described the anatomy of two northern Atlantic species (*Pandora inaequalvis* and *P. pinna*), Allen and Allen (1955) further discuss the habits of *P. inaequalvis* and Allen (1961) described

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the development of this species. Yonge and Morton (1980) have described shell and ligament structure in *P. grandis* and considered the phylogenetic affinities of the family. Boss (1978) has constructed a pandoracean paradigm and shown, using cladistics, the relationship existing between constituent families and the close affinity of the superfamily to the Thraciacea.

#### MATERIAL AND METHODS

Following dissection, the specimen of *F. ceylanica* was carefully removed from its shell, fixed in Bouin's fluid and transversely sectioned at 6  $\mu$ m. Alternate slides were stained in either Ehrlich's haematoxylin and eosin or Masson's trichrome. The shell valves have been lodged in the collections of the British Museum (Natural History) [Reg. No. B.M.(N.H.).1983102].

#### TAXONOMY

The Pandoracea Rafinesque 1815, is now generally considered to comprise four families, the Lyonsiidae Fischer 1887, Myochamidae Bronn 1862, Cleidothaeridae Hedley 1918 and the Pandoridae Rafinesque 1815 (Morton 1981). Other families earlier linked with the Pandoracea, i.e. the Thraciidae Stoliczka 1870, Periplomatidae Dall 1895 and Laternulidae Hedley 1918 (Keen 1969) are now placed in a separate superfamily—the Thraciacea (Yonge and Morton 1980, Morton 1981). According to Keen (1969), the Pandoridae comprises a single genus—*Pandora* Bruguière 1797, with five sub-genera: *Pandora*, *Foveadens* Dall 1915, *Frenamya* Iredale 1930, *Heteroclidus* Dall 1903 and *Pandorella* Conrad 1863. The characteristic features of *Frenamya* are that the secondary teeth of the left valve are united by a transverse plate and that a ligamental lithodesma is lacking. These conditions are true of the specimen here under consideration and which corresponds to the type of *Pandora ceylanica* Sowerby 1835, the type of the subgenus *Frenamya*. The species is illustrated in Hanley (1854–1858). The hinge and ligament structure of *Frenamya* is, however, sufficiently different from that of *Pandora* (Yonge and Morton 1980) to warrant separation at the generic level and the view of Iredale (1930) is upheld.

#### BIOLOGY

Shell form in *F. ceylanica* is similar to but lateral compression more extreme than that of *P. inaequalvis* (Allen 1954, Allen and Allen 1955). Although *P. inaequalvis* can be found on the surface of the sediment it is capable of burrowing and though a variety of final positions were adopted, generally *P. inaequalvis* lies shallowly buried on its concave left valve at an angle of some 40° to the sediment:water interface, with the posterior margins of the valves at the surface. Boss and Merrill (1965) similarly suggest that *P. gouldiana* is more or less limited to the surface of soft substrata. Though confirming this observation, 'numerous individuals were found lying on the sediment surface amid pebbles, cobbles and shell debris', Stanley (1970) showed that *P. gouldiana* can burrow and when buried takes up a position with the plane of commissure at an angle of 25° to 45° from the vertical. The specimen of *F. ceylanica* was kept on mud in an aquarium for seven days but never attempted to burrow. It seems possible a lifestyle similar to that of *P. inaequalvis* and *P. gouldiana* is adopted, though as with these two species, must spend much time on the surface, exposed by scour.



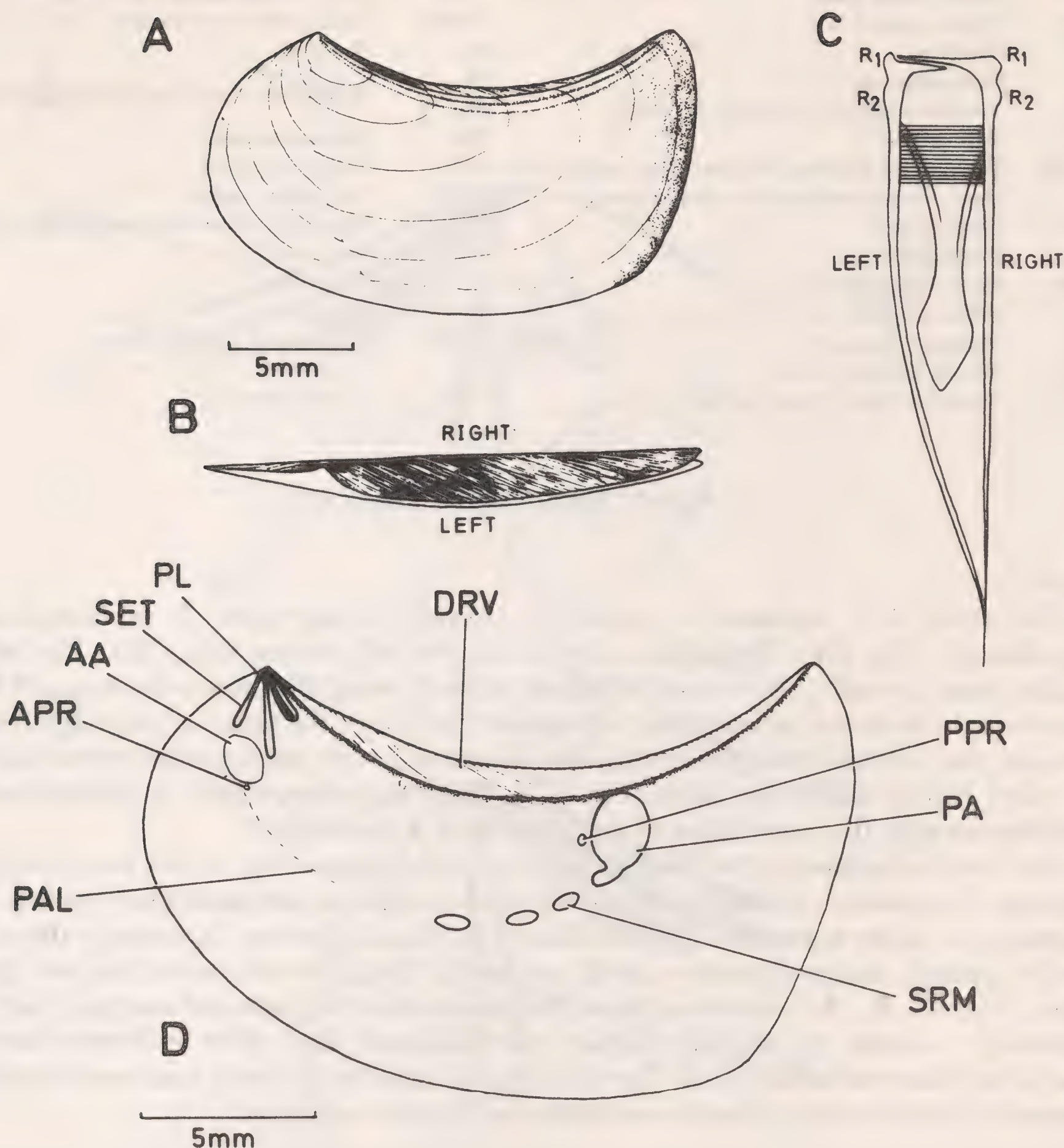


Fig. 1. *Frenamya ceylanica*. The shell as seen from A, the left and B, the dorsal aspects. C, A transverse section through the shell showing the adductor muscle and the foot and its somewhat inequilateral pedal retractor muscles. D, An internal view of the right shell valve.

#### ABBREVIATIONS USED IN FIGURES

A	Anus
AA	Anterior adductor muscle (or scar)
AOL	Anterior outer ligament layer
APR	Anterior pedal retractor muscle (or scar)
AU	Auricle
BG	Byssal groove
BYG	Byssal gland
CA	Ctenidial axis
CI	Cilia
DD	Digestive diverticula
DRV	Dorsal region of valve
ES	Exhalant siphon
F	Foot
FMMF	Fused middle mantle folds

FP	Fused periostracum
GA	Gonadal aperture
GC	Goblet cell
GUC	Guard cells
HA	Haemocoel
ID	Inner demibranch
ILL	Inner ligament layer
ILP	Inner labial palp
IS	Inhalant siphon
K	Kidney
LM	Longitudinal muscles
M	Mouth
O	Ovary
OD	Outer demibranch



OLP	Outer labial palp	PPR	Posterior pedal retractor muscle (or scar)
OMF	Outer mantle fold	PRM	Pallial retractor muscle
OV	Oviduct	R	Rectum
P	Periostracum	R <sub>1</sub>	} Ridges on dorsal region of shell valves
PA	Posterior adductor muscle (or scar)	R <sub>2</sub>	
PAL	Pallial line	RA	Renal aperture
PALID	Point of attachment of ascending lamella of inner demibranch to the visceral mass	RT	Rejactory tract
PEG	Pedal gland	SET	Secondary tooth
PEGA	Pedal gape	SRM	Siphonal retractor muscles (or scar)
PERG	Pericardial gland	ST	Statocyst
PG	Pedal ganglia	STA	Statolith
PL	Primary ligament	T	Testis
POG	Proximal oral groove	TMF	Transverse muscle fibres
POL	Posterior outer ligament layer	V	Ventricle
		VD	Vas deferens

## FUNCTIONAL MORPHOLOGY

*The shell*

The shell of *F. ceylanica* is extremely laterally compressed. It is inequivalve and inequilateral (Fig. 1A). The right valve is flat, the left convex (Fig. 1B). The left is also smaller than the right, the ventral marginal of both being exceptionally thin and brittle so that when the former is pressed hard up against the latter, the point of junction is indistinct. Dorsally, the posterior margin of each valve is bent at a right angle to the general surface, the left valve fitting under the right (Fig. 1C). Such an arrangement is similar to but not homologous with the escutcheon of the Veneridae (Carter 1967).

The anterior region of the shell is very reduced whereas that of the posterior is greatly enlarged. The postero-dorsal margin of the shell is concave and posteriorly curves upwards to produce a shape somewhat like the blade of a broad scimitar. Anteriorly the valves are closely opposed, but posteriorly slightly separated. Dorsally each valve has two distinctive ridges (Fig. 1C, R<sub>1</sub>, R<sub>2</sub>) extending from the umbones to the posterior margin. Each valve is posteriorly covered by slightly thicker periostracum that gives a brown tan to this area of an otherwise white shell. The shell valves are slightly worn and eroded posteriorly, suggesting that this area alone is not buried within the sediment.

*The hinge and ligament*

The hinge of *F. ceylanica* (Fig. 2) comprises two 'secondary' teeth (lamellae or crura) (SET) in the left valve and three in the right. All diverge from the umbones. In the left valve, the two teeth are united in part, proximally, by a septum that is a characteristic feature of the genus. These teeth interlock (X), between the two major teeth of the right valve (Y). The dorsal lip of the left valve interlocks with the third tooth and the dorsal lip of the right valve. On the anterior face of the posterior tooth of the right valve and uniting with the free surface of the left valve is a long, sunken, primary ligament (Fig. 2) comprising an inner layer (ILL) and a posterior outer layer (POL). The anterior outer layer is either so reduced as to be indiscernible or absent. The anterior and posterior dorsal shell margins are united by fused periostracum (FP) that serves as a weak 'secondary ligament' (Yonge 1976) to assist in valve alignment and to seal the dorsal region of the shell, but not to confer any opening thrust.

*The musculature*

Despite the anterior face of the shell being much reduced, the anterior and posterior adductor muscles (Fig. 1, AA; PA) are approximately equal. The anterior lies ventral to the distal ends of the hinge teeth (SET), the posterior ventral to the postero-dorsal borders of the



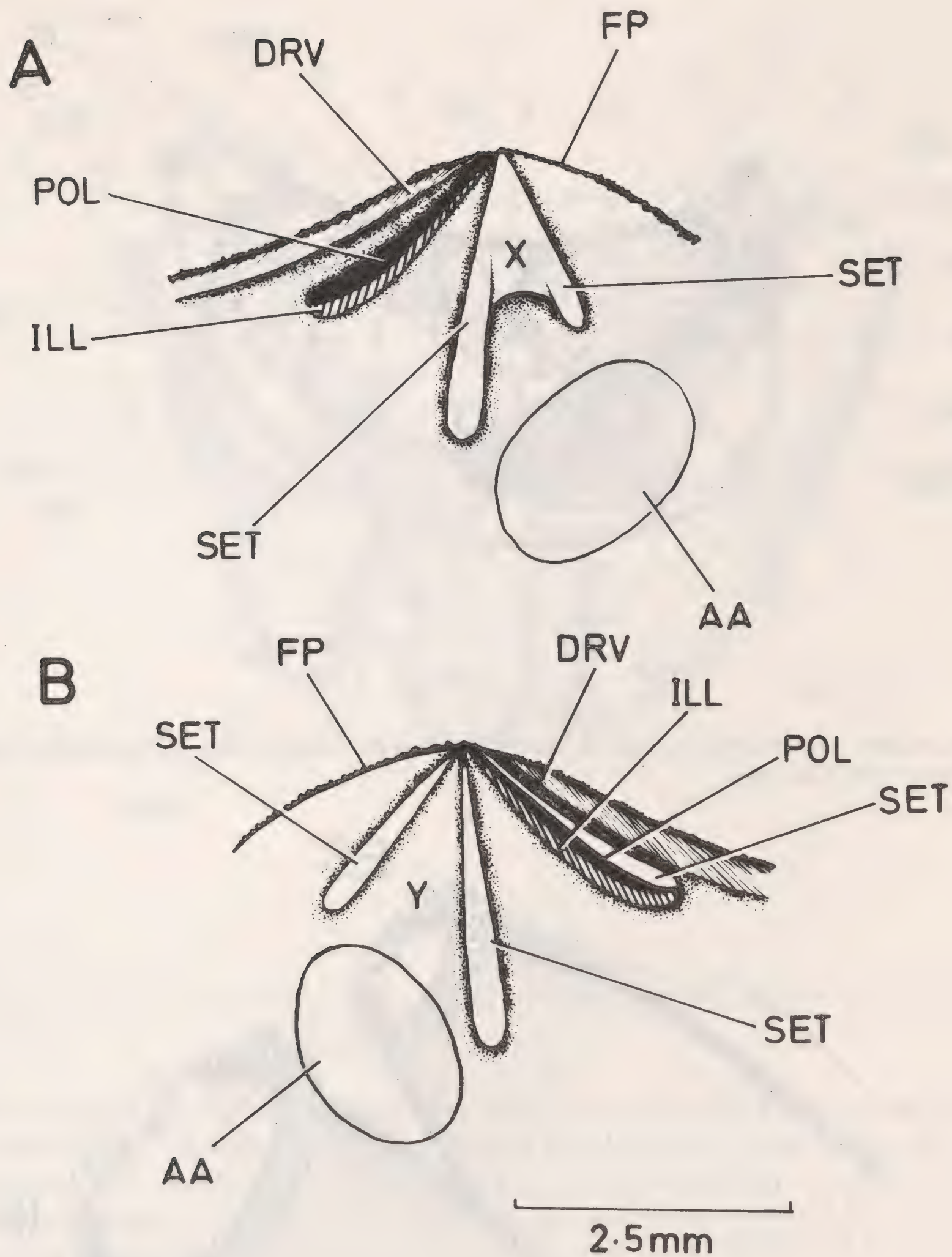


Fig. 2. *Frenamya ceylanica*. The hinge plate of A, the left and B, the right shell valves. The two teeth in the left valve (X) interlock between two other teeth in the right valve (Y). (For other lettering, see list of abbreviations).

shell (DRV). There is a tiny anterior pedal retractor muscle (APR) ventral to the anterior adductor and a somewhat larger posterior pedal retractor (PPR) anterior to the posterior adductor. The insertions of the retractors on the left valve are somewhat more dorsal to their counterparts on the right (Fig. 1C). A very faint pallial line (Fig. 1D, PAL) is distant from the shell margin. There is no pallial sinus but postero-ventrally, the pallial retractor muscles are enlarged to form four discrete blocks of siphonal retractor muscles (SRM), with large scars on the pallial line. These retract the siphons deeply between the shell valves.

#### *The siphons*

The siphons of *F. ceylanica* (Figs. 3 and 4, IS; ES) are short, extending no more than 1 or 2



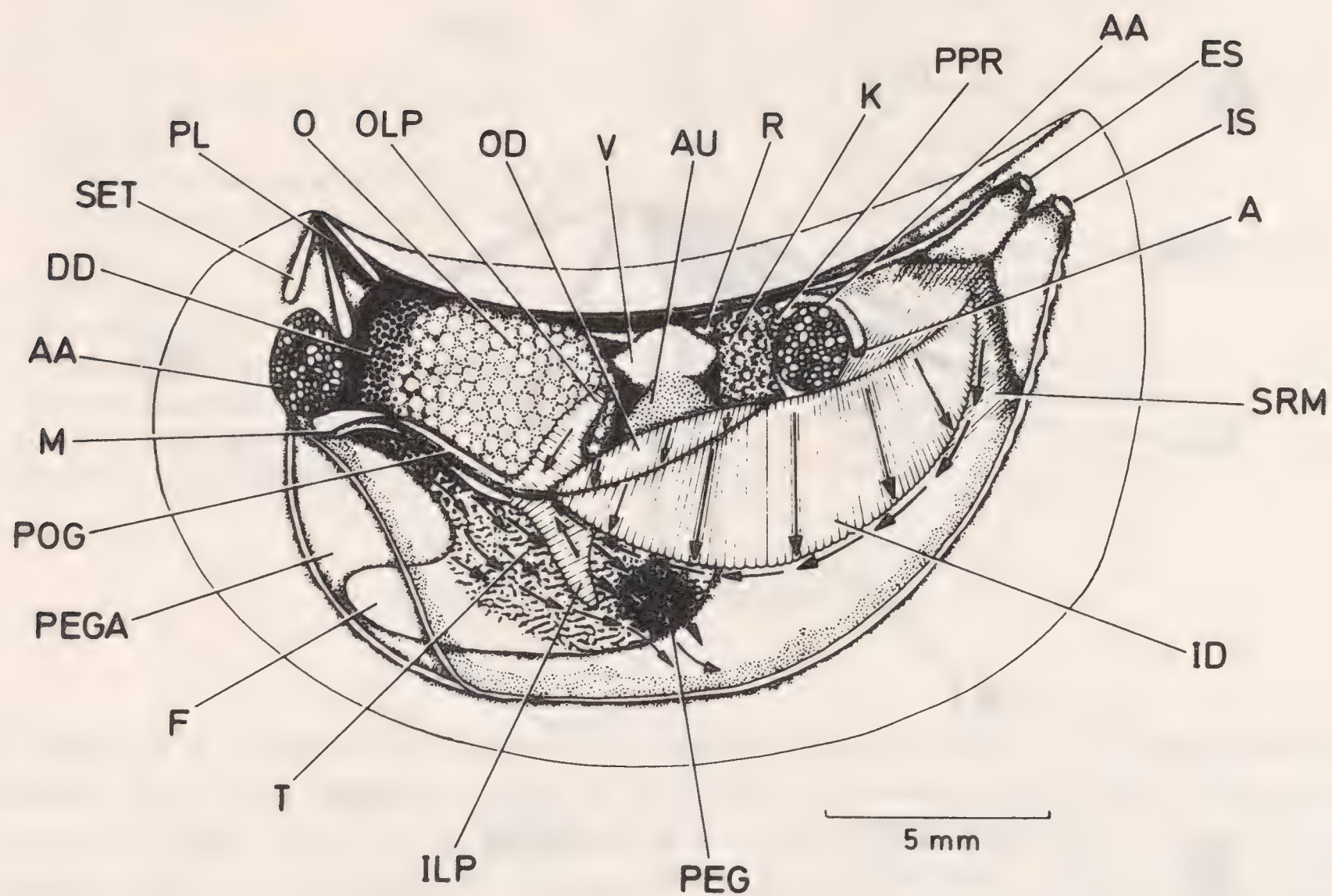


Fig. 3. *Frenamya ceylanica*. The structure and ciliation of the organs of the mantle cavity as seen from the left side. (For lettering, see list of abbreviations).

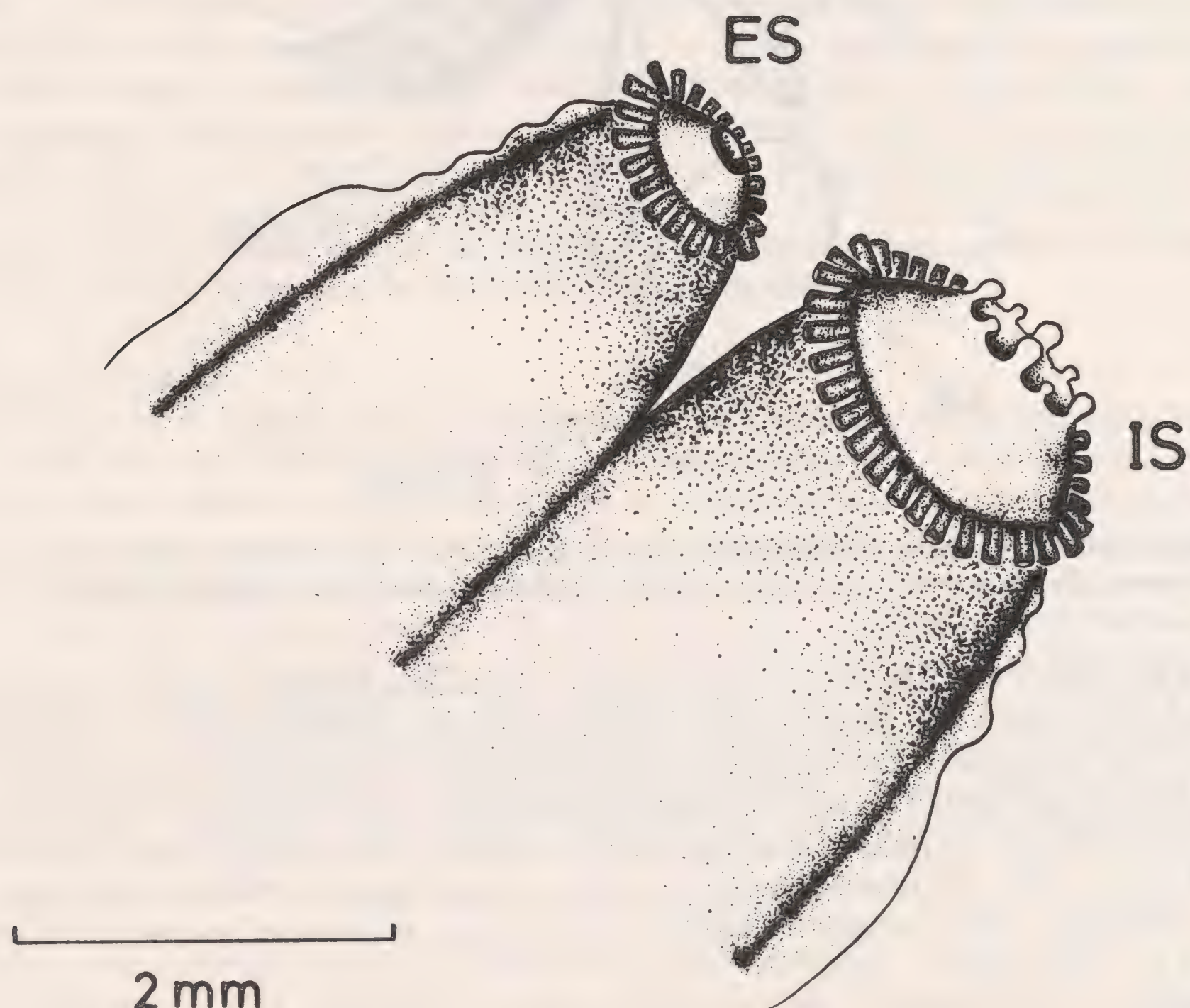


Fig. 4. *Frenamya ceylanica*. The siphons as seen from the left side. (For lettering, see list of abbreviations).



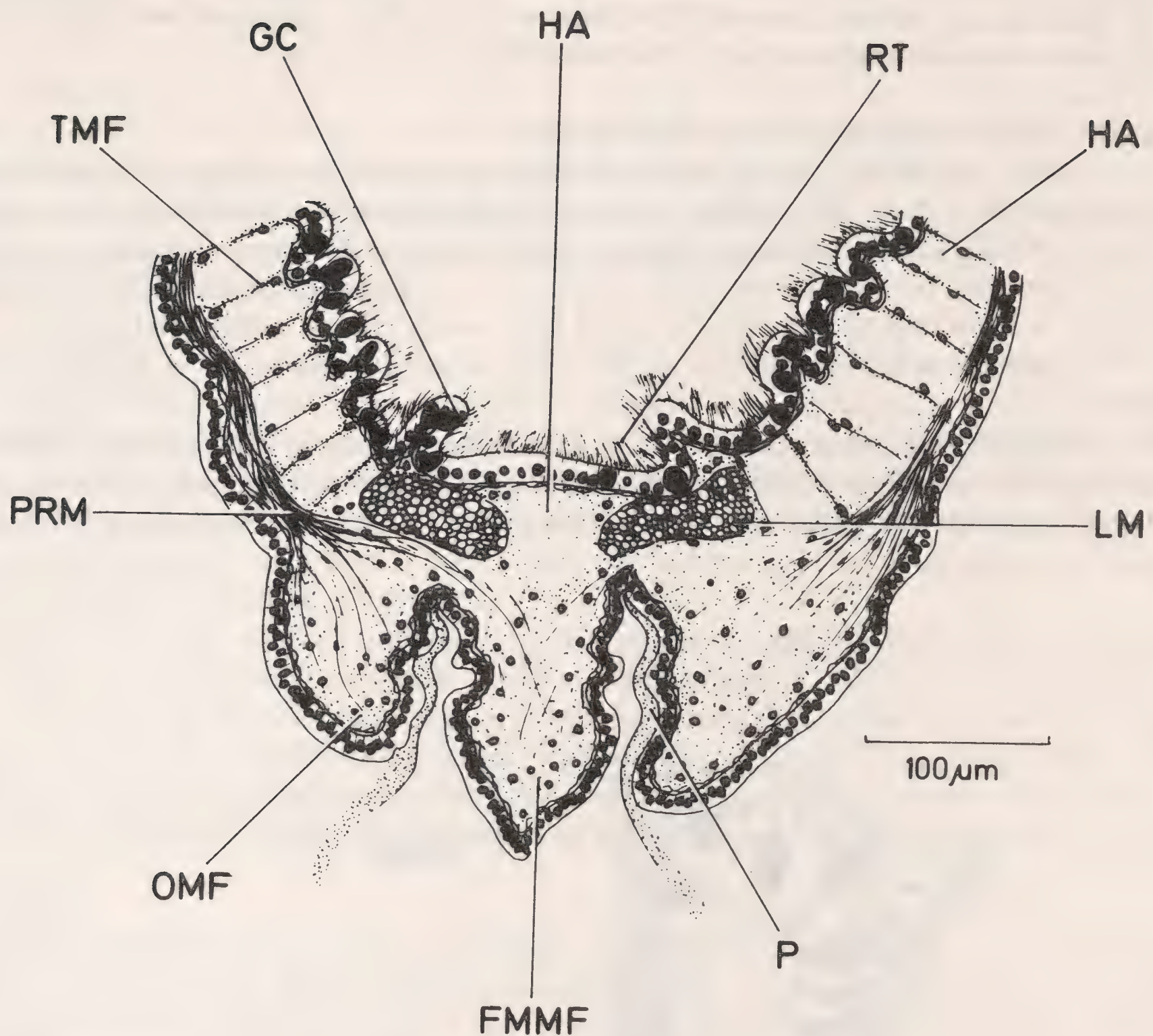


Fig. 5. *Frenamya ceylanica*. A transverse section through the ventral mantle margin. (For lettering, see list of abbreviations).

mm from the posterior valve margins. The siphons are formed by fusion of the inner and middle mantle folds (Yonge 1982) and are thus fused almost to the tip but not covered by periostracum. The smaller exhalant siphon (Fig. 4, ES) is apically surrounded by a ring of some 20 small, blunt, tentacles. The inhalant siphon (IS) is surrounded by a ring of some 40, larger, tentacles with the orifice located on a small cone distal to these. The cone is crowned by four large papillae alternating with smaller ones.

#### *The mantle margin*

The pedal gape (Fig. 3, PEGA) is extensive posteriorly, but a fourth pallial aperture often found in the Anomalodesmata (Morton 1981) is absent. Allen (1954) described the mantle margin of *Pandora inaequalvis* but did not define the degree of mantle fusion in conventional terms (Yonge 1957, 1982). In *Frenamya* (Fig. 5), fusion involves the inner and middle folds (Type B) (FMMF). The outer fold (OMF) is large. The epithelium internal to the folds is extensively ciliated ( $20\ \mu\text{m}$ ) and two rejectory tracts (RT) serve to channel pseudofaeces towards the inhalant siphon. These are bound in mucus from large ( $12\ \mu\text{m}$ ) basiphilic goblet cells (GC) located between epithelial cells.

Muscle fibres from the pallial retractors (PRM) extend into the mantle margin, and in conjunction with longitudinal muscles (LM), ensure deep retraction of the mantle edge. Expansion is by the pumping of blood into an extensive central haemocoel (HA) and into



lateral haemocoels (HA) between the pallial epithelia. Overfilling is prevented by transverse fibres (TMF) across the haemocoel. The periostracum (P) is thin and two layered as in all anomalodesmatans hitherto studied (Morton 1981).

*The organs of the mantle cavity and their ciliary currents*

The ctenidia are of the typical anomalodesmatan plan comprising a large, complete, inner demibranch (Fig. 3, ID) and the very much reduced ascending lamella only of the outer demibranch (OD). The ctenidium is heterorhabdic, eulamellibranch and plicate, each plica usually comprising ten filaments. The ciliation is of Type E (Atkins 1937). The inner demibranch is attached to the visceral mass by a weak ciliary union. Behind the visceral mass, the supra-branchial chambers of the inner demibranchs unite to form a capacious chamber.

The ctenidial/labial palp junction is of Category 3 (Stasek 1963, Morton 1981). The labial palps (ILP; OLP) are relatively small, unlike those of many other bivalves that occupy soft muds. The palps are widely separated from the mouth by extremely long proximal oral

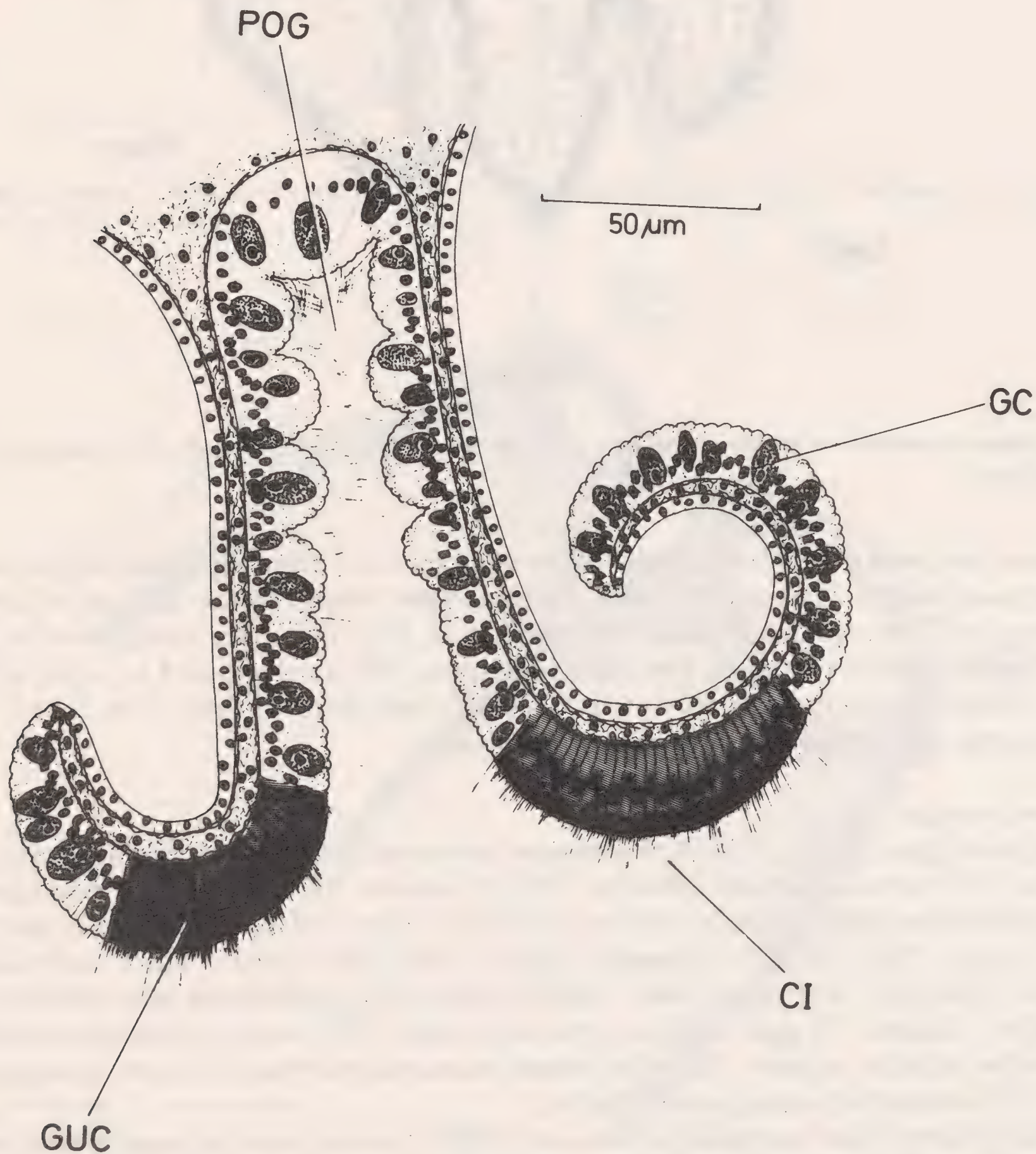


Fig. 6. *Frenamya ceylanica*. A transverse section through a proximal oral groove. (For lettering, see list of abbreviations).



grooves (POG) as in *Pandora* (Allen 1954). The outer lip of the groove is longer and overarches the inner, forming a tube within which accepted material is transported by cilia, and bound up in mucus secreted from goblet cells (GC), to the mouth, located ventral to the anterior adductor muscle (Fig. 6). The crest of each lip is lined by a columnar epithelium of guard cells (GUC) with a border of dense cilia 20  $\mu\text{m}$  long. Internally, fibrillae are clearly defined. These strong ciliary tracts presumably have a cleaning function.

On the mantle and visceral mass (Fig. 3) powerful ciliary currents are directed postero-ventrally and pseudofaeces pass to the rejectory tracts of the mantle margin (Fig. 5, RT), to be expelled from the inhalant siphon.

#### *The visceral mass*

The stomach and course of the intestine in *Pandora inaequalvis* have been described by Allen (1954). Purchon (1958) has described stomach structure in *P. inaequalvis* and shown it to be of Type IV and adapted for processing large amounts of fine material. The style sac and mid gut of *Pandora* and *Frenamya* are conjoined. In *F. ceylanica*, the rectum (Fig. 3, R) penetrates the ventricle (V) of the heart and the kidney (K) to pass over the posterior adductor (PA) and end in an anus (A).

The foot (F) is large with a byssal groove in its posterior margin. In section (Fig. 7A), the groove (BG) is surrounded by a small basiphilic byssal gland (BYG). In the visceral mass there is a very large eosinophilic sub-epithelial gland (PEG) the function of which is unknown. Dorsal to the fused pedal ganglia (Fig. 7B, PG) is a pair of statocysts (ST) some 60  $\mu\text{m}$  in diameter whose epithelium comprises cells 12  $\mu\text{m}$  in length with very fine, long, cilia. The statolith (STA) is a single, darkly staining sphere some 8  $\mu\text{m}$  in diameter.

#### *The pericardium*

The pericardium (Fig. 8) encloses a median ventricle (V) and lateral auricles (AU) each darkly coloured brown by the pericardial gland (PERG). In the postero-ventral floor of the pericardium is a pair of reno-pericardial apertures to the proximal limbs of the paired kidney. These empty via the distal limbs into the supra-branchial chamber at a renal aperture (RA) separate from the gonopore (GA). The latter receives the ovarian duct (OV) and the vas deferens (VD). *Frenamya*, as with most other anomalodesmatans, is a simultaneous hermaphrodite. The ovary (O) occupies an antero-dorsal position in the visceral mass, the testis (T) a postero-ventral. Eggs and sperm were ripe at the time of collection and similar to the telolecithal eggs of *Pandora* (Allen 1961) with an enclosing gelatinous capsule.

## DISCUSSION

*Frenamya ceylanica* is a member of the 'rare' bivalve subclass Anomalodesmata and whose other representatives are, inshore, generally adapted to rather narrow specialised microhabitats. In the deep seas they are predators (Reid and Reid 1974). Hitherto, only *Laternula truncata* and *L. anatina* have been recorded from Hong Kong, the former from mangrove muds, the latter in 7–8 metres of water (Morton 1976). *F. ceylanica* is a sub-littoral species, occurring on fine mud. As it did not attempt to burrow it might be assumed that the species lies close to the surface of the sediment. It does seem possible, however, bearing in mind the similarity in morphology and the life style of *Pandora inaequalvis* and *P. gouldiana*, that some re-burrowing is possible. In life *F. ceylanica* probably lies on its convex left valve, slightly buried, with the posterior margin at the sediment:water interface.

Anomalodesmatan characters include extensively fused mantle margins, a ctenidial structure and ciliation of Type E and simultaneous hermaphroditism (Morton 1981).



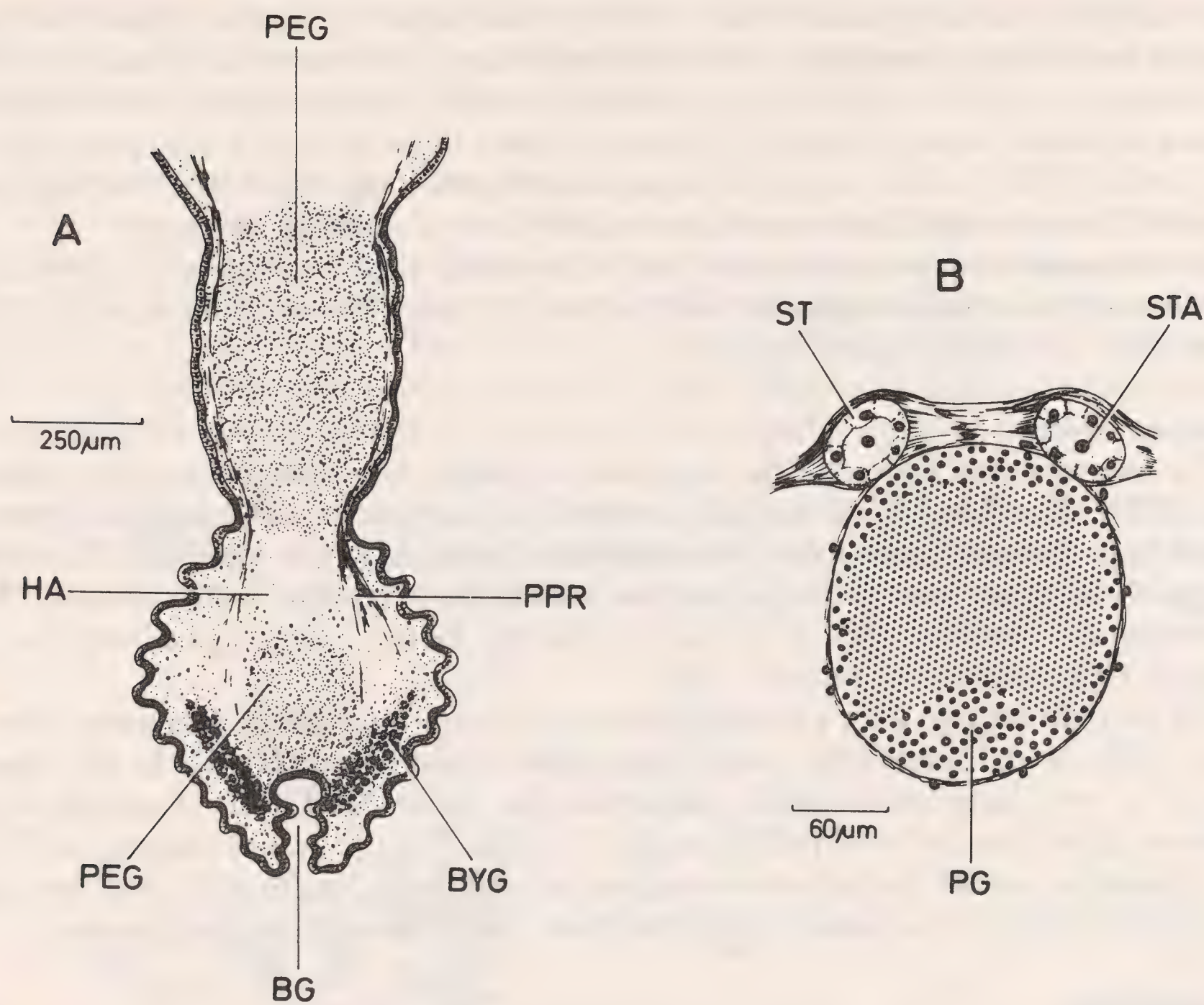


Fig. 7. *Frenamya ceylanica*. A, a longitudinal section through the foot; B, a transverse section through the pedal ganglia and the associated statocysts. (For lettering, see list of abbreviations).

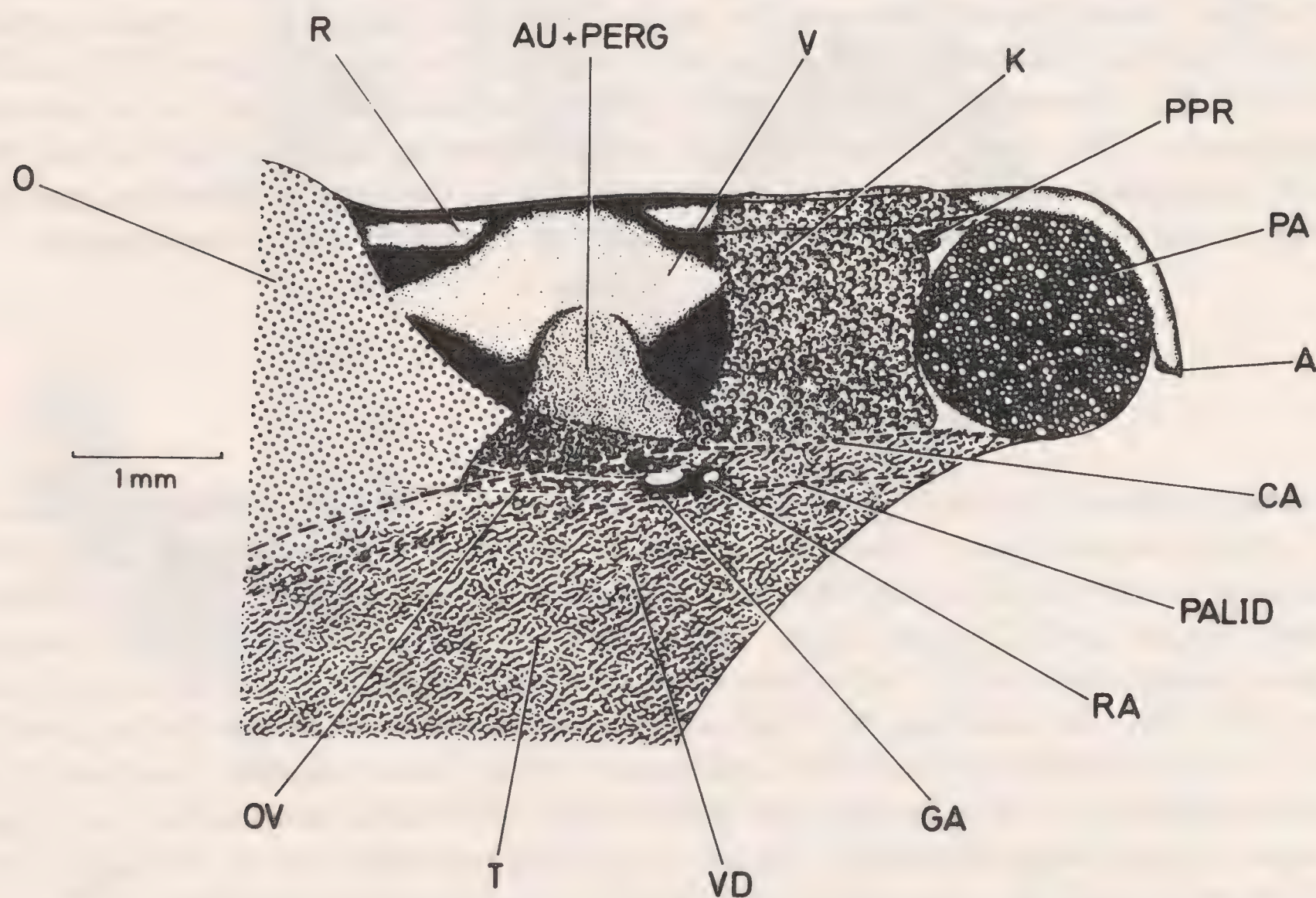


Fig. 8. *Frenamya ceylanica*. The organs of the pericardium as seen from the left side. (For lettering, see list of abbreviations).



Interest in *Frenamya*, centres around (a), the structure of the ligament and (b), adaptations to life on the surface of soft deposits.

Yonge and Morton (1980) have described the ligament of *P. grandis* and shown the hinge to comprise a number of teeth, two on the right and one on the left valve, each fitting into sockets on the opposing valve. These are secondary structures that are not homologous to the cardinal teeth of the Heterodonta. Owing to lateral compression and dorso-ventral deepening, the primary ligament is extended ventrally and in *P. grandis* comprises a large posterior outer layer, an inner layer and lithodesma and a minute anterior outer layer. In *Frenamya*, the situation is different: two teeth in the left valve interlock with two in the right, the reflected dorsal margin of the left valve interlocking with the dorsal margin of the right valve and a further tooth. These differences justify separation of *Frenamya* from *Pandora*. Such a secure interlocking system has implications with regard to the life-style of *Frenamya*. Thus, Yonge (1977) has shown for *Placuna placenta* that colonisation of surface sediments has resulted from significant structural adaptations to the shell and that lateral compression, like a disc (Fig. 9C), ensures the shell 'floats' on the surface. The discoidal form is achieved by the assumption of the monomyarian condition (Fig. 9A), with great reduction of the anterior end of the shell, and consequent loss of the anterior adductor, and inflation of the posterior. Lateral compression also results in the 'sinking' of the primary ligament and the splitting of the inner layer (Fig. 9E, ILL) so that its halves, with either anterior or posterior outer layer (AOL; POL), form a V attached to secondary teeth or crura (SET) that interlock with those of the opposite valve (Fig. 9G). A secondary ligament of fused periostracum (Fig. 9E, FP) unites the valves dorsally and assists in valve alignment as well as keeping sediment from the dorsal region of the shell valves.

The situation in *Frenamya* is similar. The bivalve is laterally compressed (Fig. 9D), the posterior end of the shell is greatly enlarged relative to the anterior (Fig. 9B), with a slight reduction in the size of the anterior adductor muscle and anterior pedal retractor. The monomyarian condition has not evolved in the Anomalodesmata (Morton 1981) but the broad scimitar shape can be seen as an attempt to increase the surface area of the shell within the constraints imposed by the dimyarian condition. Runnegar (1974) and Yonge and Morton (1980) have shown that within the Anomalodesmata there is a trend from a primitive external primary ligament towards a sunken, internal ligament. This is particularly true of the Pandoracea (Yonge 1976) and, in *Frenamya*, is associated with the dorso-ventrally aligned primary ligament (Fig. 9F, ILL; POL) which with secondarily developed teeth (SET), are functionally similar to the split primary ligament and crura of *Placuna* and which also has a 'secondary' ligament (FP) at the dorsal margin of the shell.

Other features adapting *Frenamya* to a life on soft surfaces include a mantle margin which can be deeply retracted from the borders of the shell allowing the almost perfect sealing of the mantle cavity. As in *Placuna* a byssus is absent in the adult but an extensive byssal gland and groove suggests a functional byssus is probably present in the juvenile (Allen 1961). This would act as an anchor for the juvenile in an unstable habitat. Within the mantle cavity there are powerful rejectory currents for the removal of the sediment that must enter when the bivalve is feeding. Extensive mucous glands in the mantle (and possibly the large gland in the foot) probably promote consolidation of pseudofaeces and distinct rejection tracts assist in the removal of these. A consequence of the posterior enlargement of the shell relative to the anterior, is that the palps and thus the ctenidia are distant from the anterior adductor. This is offset by the great extension of the proximal oral grooves linking palps and mouth. Such is the situation in *Pandora* too (Allen 1954). The proximal oral grooves are modified. Material is carried to the mouth in the depths of the groove, but the crests of each lip have a row of stiff cilia which presumably keep the grooves free of unsorted sediment. The ctenidium largely comprises the inner demibranch, the great reduction in the outer demibranch possibly being correlated either with the reduction of the anterior regions of the body or the compressed



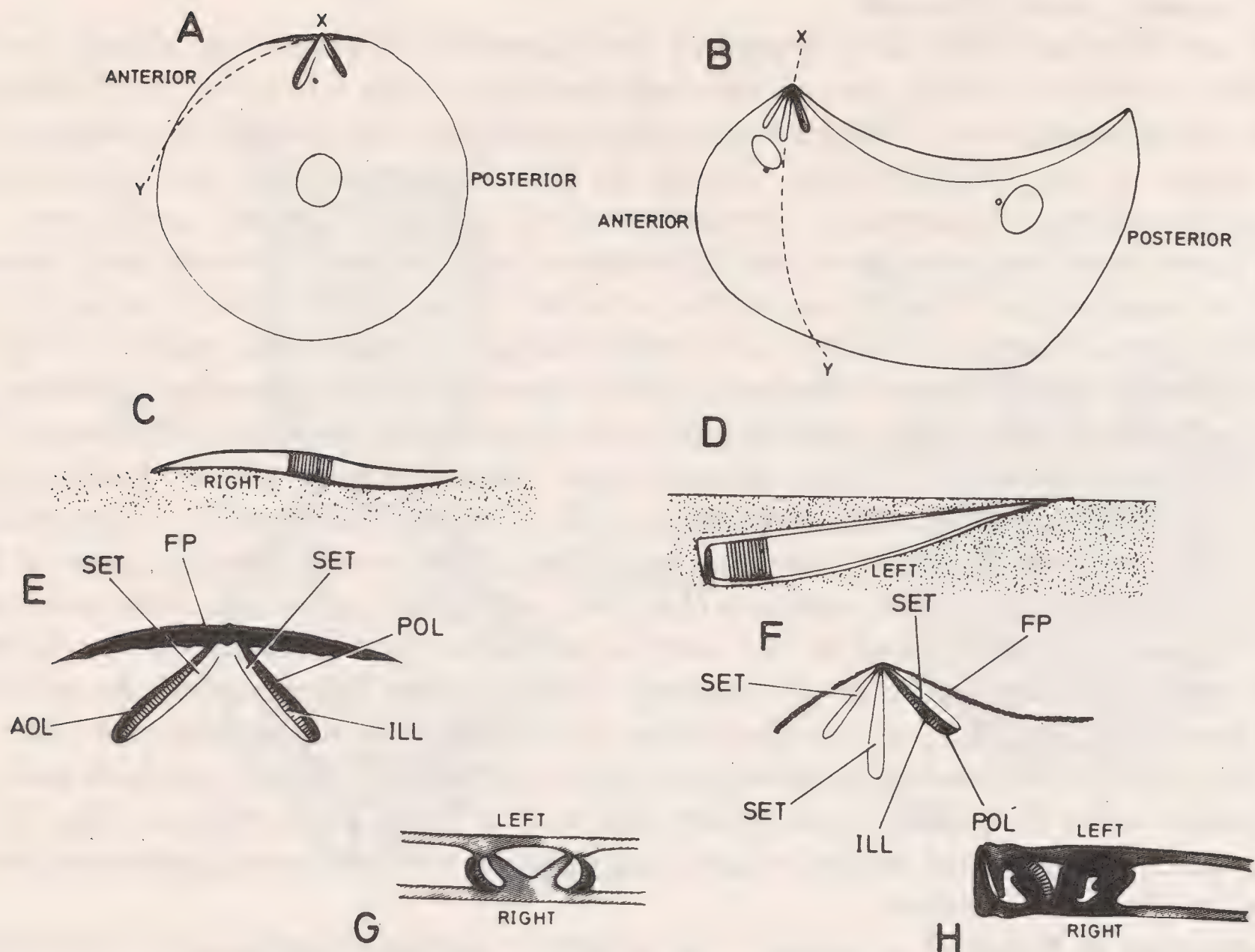


Fig. 9. A comparison of the convergent features of *Placuna placenta* and *Frenamya ceylanica* to life on the surface of soft sediments. A,B, internal views of the right shell valves (x-y is the dorso-ventral median shell axis); C,D, positions occupied on the sediment; E,F, the hinges of the right valves; G,H, transverse sections through the ligament and hinge teeth. (For lettering, see list of abbreviations). (A,C,E and G all after Yonge 1977).

form. The siphons of *F. ceylanica* rarely protrude from the posterior borders of the shell, but are deeply inset (but with no pallial sinus) and retracted by powerful muscles of the pallial line. These are probably adaptations to a high sediment load in the inhalant water.

*Frenamya* is a simultaneous hermaphrodite. Possibly also, the telolecithal eggs are incubated in the capacious supra-branchial chamber as a number of anomalodesmatans probably do (Morton 1981). Pelseneer (1911) detected early developmental stages within the ctenidia of *Pandora elongata*. Allen (1961) has shown that development of *Pandora inaequalvis* is rapid, being completed within a maximum of four days with one day in the plankton, permitting rapid recolonisation of a narrow microhabitat.

*Frenamya* can be seen as the anomalodesmatan equivalent of *Placuna placenta* (Anomiacea); convergent features facilitating surface colonisation of soft subtidal muds. Specialisation has not proceeded so far in *Frenamya* as in *Placuna* and the Pandoridae survive marginally in this environment. *Placuna* is more widely dominant on tropical shores. In more temperate northern latitudes, however, the Pandoridae are more numerous (Boss & Merrill 1965) and often the sole (bivalve) occupants of such a habitat (Allen 1954). The view of Morton (1981) regarding the Anomalodesmata as a whole is thus reinforced—they have survived in narrow niches but failed in competition for broader habitats because of the success of the reproductively simpler Pterioidea and Veneroidea.



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# TRACHYCYSTIS LAMELLIFERA (SMITH) IN TANZANIA (PULMONATA: ENDODONTIDAE SENSU LATO)

BERNARD VERDCOURT\*

(Accepted for publication, 19 May, 1984)

*Abstract:* *Trachycystis lamellifera* (Smith) is recorded from Tanzania and a fresh specimen is figured for the first time.

Amongst a collection of East African snails sent to me for examination by Dr. F. Puylaert, Musée de l'Afrique Centrale, Tervuren, Belgium was a series of a very elegant small endodontoid species clearly belonging to *Trachycystis* sensu lato. A comparison with descriptions and types of species known to occur in East Africa at first yielded no results until I realised that the exceedingly fragile wing-like lamellae (see Pl. 21) would soon wear down or even right off; bearing this in mind *T. lamellifera* (Smith) and *T. rugosa* Preston became strong candidates for the identity of the Tanzania material and detailed examination, has convinced me that they are identical. Preston described his species from material collected on Mt. Kenya probably by R. Kemp and other material referred to as var. *levior* is present in some collections but differs only in being even more worn! Material from the Holm collection on loan to me from the Natural History Museum, Stockholm is also cited.

## *Trachycystis lamellifera* (Smith)

1903 *Pyramidula lamellifera* Smith, p. 317, pl. 4, fig. 15

1911 *Trachycystis rugosa* Preston, p. 468, pl. 11, fig. 16

## DISTRIBUTION

KENYA: Mt. Elgon, S. side, Kimilili R., 2400 m., 30 Jan. 1965, Å. Holm 114 (Stockholm); Mt. Elgon E. side, 2750 m., 11 Jan. 1969, Å. Holm 130 (Stockholm); 61 km. S. of Eldoret, Timboroa, sieved in bamboo zone, 2740 m., 7 Jan. 1973, Å. Holm 282 (Stockholm); Molo, Mau Escarpment, 2150–2200 m., 11–12 Apr. 1957, Basilewsky & Leloup MRAC 788663; Mau Escarpment, 6500–9000 ft., *Doherty* (British Museum (Nat. Hist.) 1901.12.21 136–140, syntypes); Maralal, sieved in rain-forest leaf-litter 2200 m., 2 Jan. 1973, Å. Holm 273 (Stockholm); Mt. Kenya, 9000–10000 ft. (2700–3000 m.), ?R. Kemp (MRAC Tervuren holotype); British Museum (Nat. Hist.) 1911.10.12. 203–4 & 1937.12.30 2082–41 paratypes of *rugosa*; Liverpool, Salisbury Collection 1965. 141, paratype of *rugosa*) also other material labelled “Mt. Kenya, 6000–9000 ft” and a third lot “Mt. Kenya 6000–9000 ft. var *levior* (Liverpool, Salisbury Collection 1965, 141 and British Museum (Nat. Hist.) 1911.8. 22.46–47 & 1937.12. 30. 1969–71); Mt. Kenya, Kabaru Forest Station, 2250 m, 26 Feb. 1969, Å. Holm 183 (Stockholm); Mt. Kenya, Ragati Forest Station, 2000 m. 25 Mar. 1929, Å. Holm 180 (Stockholm).

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TANZANIA. Oldeani, towards E, montane forest with bamboo, 2300 m., 13 June 1957, *Basilewsky & Leleup* MRAC, 788793–788799; Ngorongoro, in the burrow of a *Tachyoryctes* (mole-rat), 2400–2500 m, 14–17 June 1957, *Basilewsky & Leleup* in MRAC 788721–788725.

A radula was mounted from a juvenile Oldeani specimen and there are about 60 rows of teeth; the 5 laterals on either side of the central tooth are very similar to it, 3-cusped with the central cusp much the largest and very strongly narrowed to the base but not completely separated. The marginals could not be observed properly with the equipment available so it is not possible to assign the species to any of the groups discussed by Watson (1934) but it resembles *Chalcocystis* and *Phortion*.

The paratypes of Smith's species are brownish perhaps due to staining whereas much of the Holm and Basilewsky and Leleup material is creamy white.

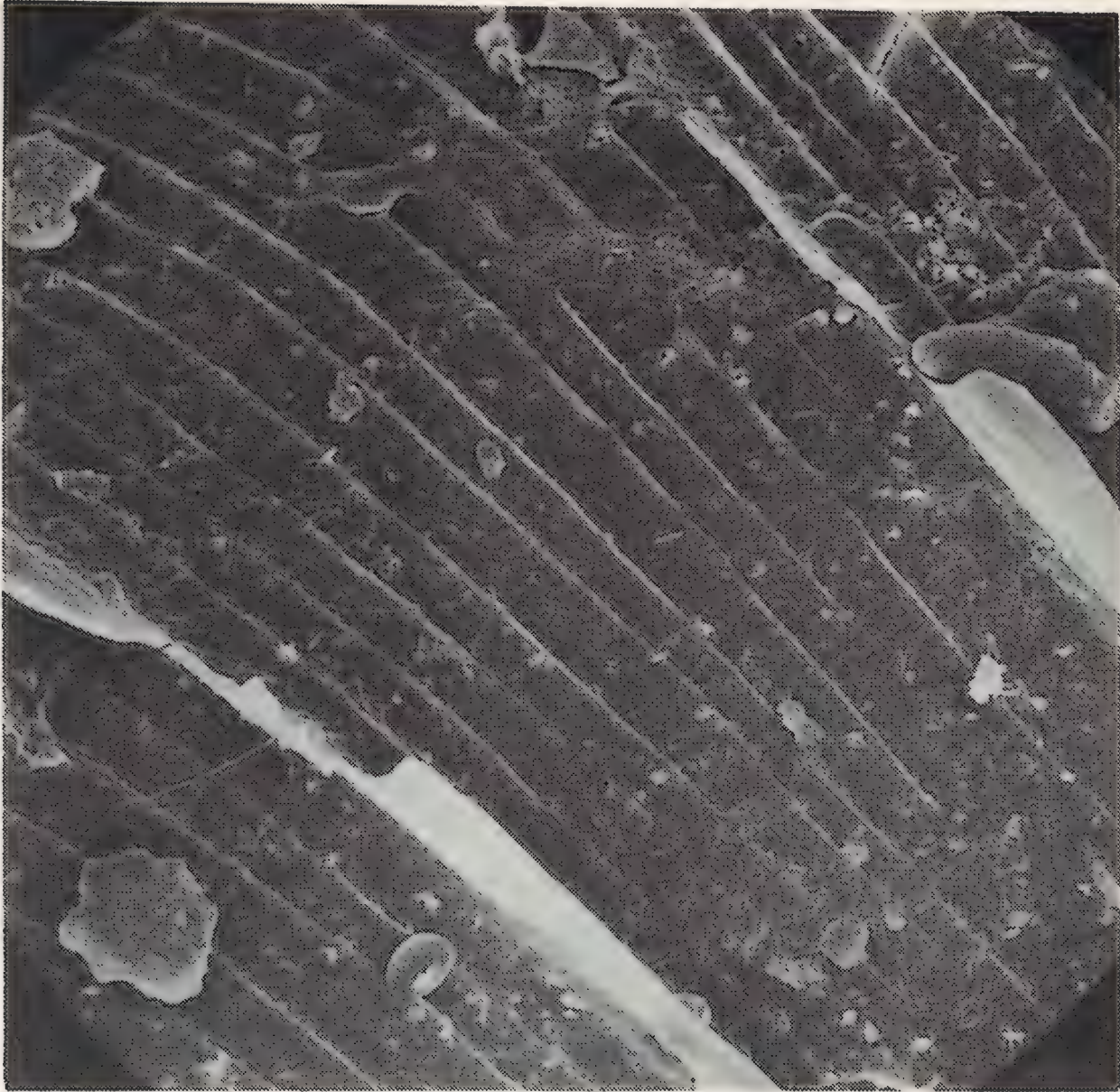
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1



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PLATE 21.

*Trachycystis lamellifera* (Smith). Fig. 1. Shell of specimen from Tanzania, Oldeani  $\times 24$ , leg. Basilewsky & Leloup MRAC 788793; Fig. 2. Sculpture of same,  $\times 660$ . S.E.M.s by Mrs. M. Harley.







# THE DIET OF INDO-PACIFIC *VASUM* (GASTROPODA: VASIDAE)

JOHN D. TAYLOR\*

(Accepted for publication, 16 April 1984)

**Abstract:** An examination of the diet of the common coral-reef gastropod *Vasum turbinellus*, based upon the gut content analysis of 280 specimens from various localities, shows a diet consisting of approximately 50% polychaete annelids and 50% sipunculans. Chaetopterid polychaetes form about 20% of the diet at most places but species of Eunicidae and Terebellidae are also common prey items. *Vasum rhinoceros*, an East African species, also eats polychaetes and sipunculans, and two individuals of the large *Vasum ceramicum* had been feeding upon eunicid polychaetes. Amongst those gastropods with which it coexists *Vasum turbinellus* overlaps in diet with species of Mitridae and *Drupa lobata* and *D. grossularia*, which are sipunculan specialists, and to a lesser extent with species of *Conus* and *Drupa morum* which feed upon polychaetes, particularly from the Eunicidae and Nereididae. No other common shallow-water gastropods seem to feed regularly upon chaetopterid polychaetes. Limited evidence from other members of the Vasidae would suggest a polychaete or a mixed polychaete/sipunculan diet.

## INTRODUCTION

The intertidal bench and hard platform habitats of Indo-Pacific coral reefs support diverse and abundant assemblages of predatory gastropods (Richard 1982, Kohn 1980, Reichelt 1982, Taylor & Reid 1984). Considerable attention has been given to the ecology of the more diverse groups of gastropods from these habitats, particularly *Conus* (Kohn 1959, 1968, Kohn & Nybakken 1975, Leviten 1976, 1978;), species of *Morula*, *Thais* and *Drupa* in the Muricidae (Bernstein 1974, Taylor 1976, 1978, 1983, 1984) and Mitridae (Kohn 1970, Taylor 1984). A large and abundant species which coexists with these other predators is *Vasum turbinellus* (Linnaeus) whose habits have received little attention.

As well as *Vasum turbinellus*, six other species of *Vasum* occur in the Indo-Pacific Province, but only one of these, *V. ceramicum* (Linnaeus), has a wide geographical distribution. Of the other species, *V. armatum* (Broderip) is common on islands in the eastern Pacific, *V. rhinoceros* (Gmelin) is found only in East Africa, *V. tubiferum* (Anton) only in the Philippines and *V. truncatum* (Sowerby) and *V. crosseanum* (Souverbie) appear to be very rare (Abbott 1959).

In this paper I report quantitative information on the diets of *Vasum turbinellus* at various localities in the Indo-Pacific, for *V. rhinoceros* from Kenya, and additionally, a small amount of information for *V. ceramicum* from Guam. The recent classification by Boss (1982) considers the family Vasidae to comprise three subfamilies, the Vasiniae, Turbinellinae and Ptychatractinae. To these, Harasewych (1983) has recently added the Columbariinae. The small amount of published information concerning these other subfamilies is also reviewed. The main objectives of the study are to determine the role of these large gastropods in coral-reef food webs and to establish areas of possible interaction with other syntopic predatory gastropods. Another broader objective in studying the diet, is to try and understand the adaptive significance of the anatomical features of the foregut, which are amongst the more important systematic characters used in separating families and determining relationships within the Neogastropoda (Ponder 1973).

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## METHODS AND STUDY AREAS

Samples of gastropods for the food analysis were cracked, or boiled and then fixed in formalin soon after collection, for later dissection in the laboratory. Stomach, rectal and oesophageal contents were removed and mounted for microscopic examination on glass slides in 'Aquamount'. In some cases faeces were collected from animals kept in dishes of seawater.

Specimens used in the study were collected at the following localities:

## Red Sea:

Sudan—Harvey Reef, a small patch reef, 3 km offshore and 14 km SSE of Port Sudan (further details in Taylor & Reid 1984).

## Indian Ocean:

Kenya—Tiwi, a narrow fringing reef site 20 km S of Mombasa.

Kenya—Shungulunzi, nr. Shimoni, a narrow intertidal bench site, 72 km. S. of Mombasa.

Aldabra Atoll—the intertidal fringing reef at Picard Island.

Addu Atoll, Maldives—the seaward reef flat and lagoon reefs of Gan Island (details in Taylor 1978).

## Pacific Ocean:

Lizard Island, Queensland—sites on the E. & S.E. of the island and also on nearby Carter Reef of the Outer Barrier Reef.

Guam—an intertidal reef flat site at the north end of Pago Bay (details in Taylor 1984).

## SIZE

Shell size information for the populations of *Vasum* sampled is given in Table 1.

*Vasum turbinellus* is amongst the larger of the reef flat gastropods. However, sizes vary considerably from place to place with the populations from Kenya and Carter Reef, Queensland, being the largest of those sampled. The largest specimen encountered, from Kenya, was of 73.2 mm shell height, although Abbott (1959), records specimens of 85 mm. The smallest population sampled was that of Pago Bay, Guam; this locality has suffered mass mortalities of reef flat animals (Yamaguchi 1975) and the *Vasum* may be fairly recent recruits.

*Vasum ceramicum* is the largest of all the Indo-Pacific reef living vasids and the two individuals collected here measured 90.3 & 95.8 mm. However, specimens much larger than this are common in museum collections and Abbott (1959) reports average sized specimens of 125 mm and large individuals at 148 mm.

## HABITAT AND ABUNDANCE

*Vasum turbinellus*

This species is one of the most abundant of the larger gastropods inhabiting intertidal and shallow hard substrate habitats on Indo-W. Pacific coral reefs. Although it may be found in a variety of habitats, including sand, marine grass beds and rubble, it is most abundant upon the rock platform substrates. There are surprisingly few studies of the quantitative distribution of molluscs on reefs; Table 2 summarizes data from a variety of localities around the Indo-W. Pacific. Population densities reach as high as 1.6/m<sup>2</sup> at Pago Bay, Guam, but average around 0.27/m<sup>2</sup> on other reefs. At most of these localities *V. turbinellus* co-occurs with other predatory gastropods, mainly species of *Conus*, *Drupa*, *Morula*, and *Mitra*.



TABLE 1

Sizes of *Vasum* sampled

Locality	Mean shell height (& standard deviation)	sample size
<i>Vasum turbinellus</i>		
Sudan-Harvey Reef	43.2 (7.8)	26
Kenya-Shungaluzi	58.5 (7.9)	30
Addu Atoll-Gan	32.5 (7.2)	36
Lizard I., Qld.	38.7 (8.4)	49
Carter Reef, Qld.	59.2 (5.1)	47
Guam-Pago Bay	28.6 (7.6)	60
<i>Vasum rhinoceros</i>		
Kenya-Tiwi	52.5 (7.5)	71
<i>Vasum ceramicum</i>		
Guam	90.3, 95.8	2

TABLE 2

Abundance of *Vasum turbinellus* in some coral reef habitats around the Indo-W. Pacific

Location & habitat	Area sampled (m <sup>-2</sup> )	Mean (per/m <sup>2</sup> )	Reference
Port Sudan: Harvey Reef			
reef top, rock pinnacles	33.5	0.12	Taylor & Reid (1984)
rock platform with some 'coral	30.0	0.07	Taylor & Reid (1984)
Aldabra Atoll			
exposed reef platform	23.5	0.13	Taylor (1976)
reef flat boulder edge	17.0	0.06	Taylor (1976)
Addu Atoll			
mid-reef flat rock	21.5	1.6	Taylor (1978)
reef flat grass bed	10.0	0.2	Taylor (1978)
Heron Id., Qld.			
reef crest	700.0	0.04	Reichelt (1982)
Guam—Pago Bay			
reef platform	14.75	0.5	Taylor (1984)
reef platform	12.0	0.4	Zipser & Vermeij (1980)
Eniwetak			
rock bench without refuges	87.0	0.018–0.45	Kohn (1980)
bench with natural refuges	20.0	0.35	Kohn (1980)
bench with artificial refuges	57.0	0.28	Kohn (1980)
bench with refuges containing sand and/or rubble	44.0	0.033–0.57	Kohn (1980)
bench with algal turf	223.0	0.013	Kohn (1980)
bench with algal turf	75.0	0.093	Kohn (1980)

*Vasum rhinoceros*

This species is common on Kenyan fringing reefs and is most abundant in areas of sand or rubble, covered in growths of the seagrasses *Thalassia* and *Thalassodendron*. An area of 65 m<sup>2</sup> of



this habitat was sampled at Tiwi with *V. rhinoceros* occurring at a density of 0.18/m<sup>2</sup>. It occurs together with other gastropods including *Strombus decorus*, *Strombus mutabilis* and *Conus lividus*.

#### *Vasum ceramicum*

Only qualitative information is available for this species which lives mainly on the fronts and slopes of fairly exposed reefs but is occasionally found upon reef edge and algal ridge habitats (Eldredge *et al.* 1977, Richard 1982 and personal observations).

#### *Vasum armatum*

This eastern Polynesian species has been shown by Kay (1971) to be common in some intertidal seaward reef flat habitats around Fanning Island (Line Islands). Richard (1982) however does not mention the species in his accounts of the molluscs of French Polynesia.

### DIET

#### *Vasum turbinellus*

The results of the gut content analysis are summarized in Table 3. 280 of the specimens dissected contained food and 336 prey items have been identified. At most localities, at least 50% of the food items recovered are sipunculan worms, with polychaete annelids making up the rest of the diet. The only exceptions were the ophiuroid remains found in one individual and two others which contained the bones and scales of small fish.

The sipunculan species eaten are mainly from the families Aspidosiphonidae and Phascolosomidae with a few from the Sipunculidae. Species from the two former families comprise most of the sipunculans living in hard substrate habitats of reef flats. Particularly important prey species are *Paraspidosiphon brocki* and *Phascolosoma nigrescens*.

Although *Vasum turbinellus* will eat a wide range of polychaete worms, species of the family Chaetopteridae usually make up a large part of the diet. The small *V. turbinellus* from the reef flat at Pago reef, Guam, consume the small species *Mesochaetopterus minutus* (around 15 mm length), whilst at other localities the larger species of *Phyllochaetopterus* (50–100 mm) are the preferred prey. As well as chaetopterids 19 other species from 9 polychaete families are eaten, although species of the polychaete families Eunicidae and Terebellidae, in particular *Loimia medusa*, are the more important prey.

The Guam population of *V. turbinellus* consumes a much wider variety of prey species than those at other places; this may be because there is a greater diversity of polychaetes available of acceptable food size for these smaller predators.

#### *Vasum rhinoceros*

Food items were recovered from 53 individuals of *Vasum rhinoceros* from Tiwi, Kenya, and the results shown in Table 4. As with *V. turbinellus* the diet mainly consists of polychaetes (71%) and sipunculans (22%) with small numbers of decapod crustacea (7%). Species from six families of polychaetes are eaten, but 33% of food items consist of the capitellid *Dasybranchus caducus*, with maldanids, *Onuphis eremita* and the terebellid *Liomia medusa* as lesser items. The sipunculans eaten are all from the families Aspidosiphonidae and Phascolosomidae. The decapod remains are all the same species of pontoniid prawn.

#### *Vasum ceramicum*

Only two food items were recovered from two individuals from Guam, both of which contained the setae of the eunicid polychaete *Eunice afra*.



TAYLOR: DIET OF *VASUM*

TABLE 3

Food items recovered from *Vasum turbinellus* at various localities in the Indo-Pacific

Prey	Port Sudan	Kenya	Aldabra	Addu	Lizard I.	Guam
<b>POLYCHAETA</b>						
Spionidae:						
<i>Polydora</i> sp.						2
<i>Laonice</i> sp.				1		
Chaetopteridae:						
<i>Phyllochaetopterus aciculigerus</i>	3					
<i>Phyllochaetopterus verrilli</i>			1	21	28	3
<i>Mesochaetopterus minutus</i>						30
Chaetopteridae sp.			2			
Cirratulidae:						
<i>Dodecaria</i> cf. <i>fisticola</i>	1					
Capitellidae:						
Capitellidae sp.					1	
Aphroditidae:						
<i>Lepidonotus</i> sp.				1		
Syllidae:						
Syllidae sp.					1	
Nereididae:						
Nereididae sp.						2
Amphinomidae:						
<i>Eurythoe complanata</i>						1
Eunicidae:						
<i>Palola siciliensis</i>						3
<i>Eunice afra</i>		5				4
<i>Marphysa</i> sp.						1
<i>Lysidice collaris</i>	1					3
<i>Nematonereis unicornis</i>				1		1
Eunicidae spp.				1		3
Sabellariidae:						
<i>Idanthyrus pennatus</i>			1			
Terebellidae:						
<i>Terebella ehrenbergi</i>						1
<i>Liomia medusa</i>	7				11	1
Terebellidae sp.			1			1
Serpulidae:						
<i>Spirobranchus</i> sp.					1	
<b>SIPUNCULA</b>						
Sipunculidae:						
<i>Siphonosoma australe</i>					1	
<i>Siphonosoma</i> cf. <i>cumane</i>	1					
<i>Siphonosoma</i> sp.					1	
Aspidosiphonidae:						
<i>Aspidosiphon brocki</i>	1			12		63
<i>Paraspidosiphon steenstrupi</i>				2		
<i>Cloeosiphon aspergillus</i>					3	
Phascolosomatidae:						
<i>Phascolosoma nigrescens</i>			1	11	48	5
<i>Phascolosoma pacificum</i>						1
<i>Phascolosoma perlucens</i>				2	1	
<i>Phascolosoma scolops</i>					7	2
<i>Phascolosoma stephensoni</i>		8		7		
<i>Phascolosoma</i> sp.						3
Sipuncula indet.	2			4	2	1



TABLE 3 *continued*

Prey	Port Sudan	Kenya	Aldabra	Addu	Lizard I.	Guam
ECHINODERMATA						
<i>Ophiocoma</i> plates						1
CARRION						
Fish bones & scales			1	1		
NUMBER OF SPECIMENS WITH FOOD	16	13	4	58	70	119
PREY ITEMS RECOVERED	16	13	6	64	105	132
NUMBER OF PREY SPECIES	7	2	6	12	12	21
% Sipunculans in diet	25	62	50	59	60	57
% Chaetopteridae in diet	19	0	33	33	27	25

TABLE 4

Food items recovered from *Vasum rhinoceros* from Tiwi, Kenya

## POLYCHAETA

## Chaetopteridae

*Phyllochaetopterus verrilli*

2

## Capitellidae

*Dasybranchus caducus*

18

## Maldanidae

*Euclymene* sp.

4

Maldanidae sp.

1

## Scalibregmidae

*Parasclerocheilus branchiatus*

2

## Onuphidae

*Onuphis eremita*

6

## Terebellidae

*Liomia medusa*

6

## SIPUNCULA

## Aspidosiphonidae

*Paraspidosiphon ?cumingi*

1

*Paraspidosiphon steenstrupi*

3

*Cloeosiphon aspergillus*

2

## Phascolosomatidae

*Phascolosoma nigrescens*

2

Sipuncula (indeterminate)

4

## CRUSTACEA

## Palaemonidae

Pontoniinae sp.

4

Number of specimens with food

53

Number of prey items

55

## DISCUSSION AND CONCLUSIONS

It is interesting to compare the diet of *Vasum turbinellus* with that of the other predatory prosobranch gastropods with which it commonly coexists. As has been mentioned above, species of *Conus*, Muricidae and Mitridae are the most abundant of the syntopic predators. Most of the reef flat species of *Conus* are polychaete feeders, specialising upon prey from the two families Nereididae and Eunicidae (Kohn 1959, 1968, Kohn & Nybakken 1975, Leviten 1976, 1978), although some, such as *Conus lividus*, feed upon Terebellidae. Although *V. turbinellus* will feed on a wide variety of polychaetes, species of the family Chaetopteridae are



much the most frequent, comprising over 20% of the diet in most samples. These large mucilaginous tube worms, which can be common at some localities (Kohn & Lloyd 1973, Reichelt 1979), are not generally eaten by other reef gastropods. They do however, form an important part of the diet of the deeper water cymatiid *Distorsio reticulata* (Taylor 1982) which inhabits soft substrates. Additionally, Harasewych (1983) reports them from the deep-water columbariid *Fulgurofusus*.

In addition to *Conus*, polychaetes are important items in the diet of other abundant predatory gastropods inhabiting the reef flat, such as *Drupa morum* and *D. rubusidæus* which are similar to *Conus* in being food specialists, mainly upon species of Eunicidae and Nereididae (Taylor 1983). *Bursa bufonia* also includes eunicid polychaetes in its more generalised diet (Taylor 1978).

Sipunculans form over 50% of the diet in *Vasum turbinellus* but are one of the less diverse phyla. However, they are abundant in coral reef habitats, for instance Bernstein (1974) reports densities of 700–1895/m<sup>2</sup> for the algal ridge at Enewetak and densities between 470–740/m<sup>2</sup> have been recorded by Kohn (1970) from marine benches at Hawaii. Additionally, densities of 3335/m<sup>2</sup> and 714/m<sup>2</sup> were recorded from Pago reef at Guam (Taylor unpublished). A number of other predatory gastropods include sipunculans as important items in their diet. All the species of coral-reef Mitridae so far examined (e.g. *M. litterata*, *M. brunnea*, *M. cucumerina*, *M. fraga*, *M. paupercula* and *Imbricaria* spp.), are specialist predators upon sipunculans and feed upon the same species as those taken by *Vasum* (Kohn 1970, Bernstein 1974, Taylor 1978, 1984). Two other specialist sipunculan feeders from the Muricidae are the similar, but geographically separated species *Drupa grossularia* and *D. lobata* (Taylor 1983). Additionally, *Bursa bufonia* includes sipunculans in its mixed diet.

The diet of *Vasum rhinoceros* is essentially similar to that of *V. turbinellus* but instead of chaetopterid polychaetes it consumes a larger proportion of sand-living polychaetes, such as the capitellid *Dasybranchus caducus*, and species of Maldanidae. Additionally, a small number of decapod crustacea are eaten.

The only information available concerning the diets of other Indo-Pacific Vasinæ is that for *Tudicula armigera* from Queensland (kindly supplied by Dr. P. W. Arnold, James Cook University, Qld.). Out of 29 individuals of this species examined, 17 food items were identified, all of them polychaete worms. Seven *Tudicula* contained setae of species from the polychaete family Pectinariidae, six contained setae of Flabelligeridae and four the setae of Chaetopteridae. There is unfortunately no published information of the diets of any of the Caribbean species of *Vasum*.

Amongst the other gastropod subfamilies considered related to *Vasum* there is only a small amount of qualitative information. The Indian chank *Turbinella pyrum* is known to feed upon terebellid and eunicid polychaetes (Hornell 1915, Moses 1923). Two out of sixteen specimens of the West Indian chank *Xancus angulatus* Solander were observed regurgitating the sipunculan *Siphonosoma* (Edwards 1970, also reported in Kohn 1975). Recently Harasewych (1983) reports the rectal contents of the columbariid *Fulgurofusus brayi* from around 275 m in the Caribbean as containing large numbers of setae from the polychaete families Serpulidae and Chaetopteridae.

On the basis of this evidence, one might extrapolate from the data for *Vasum turbinellus* and *V. rhinoceros* and suggest that a diet of polychaetes or mixed polychaetes and sipunculans is probable for all members of the Vasidae.

#### ACKNOWLEDGEMENTS

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# PROCEEDINGS OF THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

## REPORT OF THE COUNCIL 1983–1984

It is with regret that the Society has to report the death of one member; Mr. A. Stiva who joined in 1979.

The total membership of the Society now stands at 618 and is comprised of the following categories:— Full members 461, Full life members 35, Family members 49, Family life members 6, Honorary members 5, Junior members 23, Institutional members 39, total 618.

*Resignations:* Full members 24, Junior members 5, total 29.

*Struck off for non-payment of subscription:* Full members 23, Junior members 2, total 25.

*New members nominated & elected during 1983/4*

Full members 41, Family members 2 (+ 2 transfers from full membership), Junior members 5, total 52. 1 Junior member was transferred to full membership.

### *Meetings*

There were 7 Ordinary meetings held in the Demonstration Room of the British Museum (Natural History), together with one Annual General Meeting. The meeting in December was disrupted due to a bomb scare.

### *Publications*

Two parts of the *Journal of Conchology* were issued (Volume 31, parts 3 & 4) Four issues of the *Conchologists Newsletter* were printed & issued with the Annual Programme of events. No papers for students were issued.

### *Subscribers*

The total number of subscribers is 149, who took out 161 subscriptions to the *Journal of Conchology* (after 15 cancellations). There were 12 subscribers to the *Conchologists Newsletter* and *Papers for Students*.

## TREASURER'S REPORT

The Society's accounts show an exceptionally high surplus for the year of £4,906.43. A large portion of this is attributable to the anonymous donation of £2,200 10¼% Exchequer Stock, 1995. This has been acknowledged in the Society's publications and our gratitude to the generous donor expressed. In addition a substantial saving has been achieved by refraining from issuing annual Members' lists in 1982 and 1983; a new List is currently in the press. A further (unintentional) saving has occurred because of unfortunate delays in the publication of *Papers for Students*, but a number of these are expected shortly.

The investment in £875 Spillers' 7% Debenture Stock was repaid, with a capital gain of £121.18. The proceeds, together with those of the Mersey Docks and Harbour Board Stock (repaid in 1982) and funds from the bank deposit have been re-invested in £1980 10¾% I.C.I. Stock 1991/96.

Expenses and Subscriptions remained very similar to those for 1982, and sales of publications have maintained a high level. Covenanted Subscriptions increased slightly, and the Society is grateful to the Members whose covenanted Subscriptions produced the useful sum of £266.18.

24 Ordinary Members, 2 Institutional Members and 5 Junior Members are in arrears with 1983 Subscriptions. No further publications can be sent to these until payment has been made, although any which have been withheld will be sent upon receipt of the arrears.

Some bankers' orders have still not been amended to the current subscription rates, and Members are asked to note that the Council has decided that in future publications will only be sent to Members whose Subscriptions have been paid in full.

As the Society's bank has announced that Foreign cheques are now subject to a *minimum* conversion charge of £3.00 each we are obliged to request that all future payments to the Society be made in £ Sterling.



THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

Publications:-					
Newletter .....	2,408.94				Fees and Subscriptions:-
					Membership Fees .....
					Subscriptions .....
					Entrance Fees .....
					<u>8,592.47</u>
Journal:-					
Volume 31 No. 3 .....	2,347.19				Donations:-
Volume 31 No. 4 .....	2,612.67				£2,200 10¼% Exchequer Stock
Back Numbers Bought .....	22.00				Various .....
	<u>4,981.86</u>				
Printing, Stationery and Postage ...	498.41				Sales:-
Officers Expenses .....	332.27				Papers for Students .....
Meetings .....	165.00				Special Publication .....
Subscriptions .....	8.00				Journal .....
					Newsletter .....
					Atlas .....
					Shell Kits .....
					Advertising .....
					Sundries .....
					<u>629.97</u>
					Capital Gain on Repayment of
					£875.00 Spillers 7% Debenture
					Stock .....
					121.18
					Investment Income:-
					General Account .....
					Life Members Fund .....
					Reserve and Research Fund .....
					<u>1,877.51</u>
					Transfer to Reserve and
					Research Fund .....
					285.82
					<u>1,591.69</u>
					<u>£13,300.91</u>



## BALANCE SHEET AS AT 31st DECEMBER 1983

Creditors and Accrued Charges	...	1,442.17	Cash at Bank:— Current Account .....	1,743.71
Fees and Subscriptions in Advance		1,263.96	Deposit Account .....	2,434.19
Life Membership Fund .....		2,890.00	Post Office Savings Bank .....	6,065.61
				<hr/>
				10,243.51
Reserve and Research Fund .....		2,344.06	Investments:— £400 5% Treasury Stock 1986/89 2514 Units M. & G. Dividend Fund £400 14½% Loan—City of Norwich £800 5½% Loan—London County Council .....	344.00 1,522.06 400.00 769.20
			1620 Save and Prosper Units £700 Bury—13% Loan .....	892.95 700.00
			£800 15½% Treasury Stock 1998 £73.84 Subordinated Loan Stock— Mersey Docks & Harbour Board 104 10p Ordinary Shares—Mersey Docks & Harbour Board	768.00  73.84  10.40
			£2340 7¼% Whitbread Stock 1995/9 £2200 10¼% Exchequer Stock £1980 10¾% I.C.I. Stock 1991/96	1,498.38 2,200.00 1,996.09
				<hr/>
				11,174.92
				<hr/>
				£21,418.43
				<hr/>
L. LLOYD-EVANS } W. F. EDWARDS }	Hon. Auditors			MARJORIE FOGAN Hon. Treasurer
8.2.84				



JOURNAL OF CONCHOLOGY, VOL. 31, NO. 6  
RECORDER'S REPORT: NON-MARINE MOLLUSCA

A. Grid mapping

Preparations are now well advanced for a new edition of the non-marine *Atlas*. The 1984 season is likely to be the last available for contributory fieldwork. Unlike the 1976 edition, the new edition will show date-classes (generally pre- and post-1965) on all maps. There will be an explanatory text to accompany each map describing habitat, changes in distribution, and conservation problems.

B. Vice-comital records

The following new records have been verified since the last Report (*J. Conch., Lond.* **31**, p. 255). All date from 1983, unless stated otherwise.

- Cornwall East (2): *Lymnaea auricularia*, Bude Canal (21/2104); *Boettgerilla pallens*, St Austell (20/0052), both J. Humphreys.
- Somerset North (6): *Viviparus contectus*, Ashcott Corner (31/4539), Miss H. Scott.
- Dorset (9): *Hygromia cinctella*, Weymouth (30/6880), I. C. Cross, 1982.
- Hants South (11): *Hydrobia stagnorum*, Farlington Marshes (41/6803; dead shells), A. J. Jeram.
- Sussex West (13): *Physa acuta*, Sidlesham (40/8596), Miss M. B. Seddon.
- Kent East (15): *Leiostryla anglica*, Faversham (61/06), Miss E. B. Fairbrass, 1878 (Perth Museum).
- Kent West (16): *Boettgerilla pallens*, Lesnes Abbey Wood (51/4578), M. P. Kerney.
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The following are among the more interesting new records:

*Hydrobia stagnorum* (Gmelin). This species has only recently been shown to be distinct from *H. ventrosa* (Montagu) (*Basteria* **43** (1979), p. 51). Dead shells from a brackish lagoon at Farlington, near Portsmouth, have been verified by Dr. L. J. M. Butot, constituting the first British record. The shells were recovered by Mr. Jeram from a sediment core, which showed that *H. stagnorum* was present from about 1770 (when the lagoon was created) until about 1960–70, when the species died out. *Potamopyrgus jenkinsi* is the only hydrobiid living in the lagoon today. It is hoped that *H. stagnorum* may now be recognised alive in the British Isles. In the Netherlands it is much rarer than *H. ventrosa*, and seems to be declining.

*Lymnaea stagnalis* (L.), *Lymnaea auricularia* (L.). These calciphile species are unexpected on the Cardigan coast, some 40 miles from any other Welsh occurrences. Both populations are in stabilised dunes, on shell sand. The ditch at Ynyslas containing *L. stagnalis* was created only a few years ago.

*Vertigo alpestris* Alder. Two further Scottish sites, in Aberdeenshire and Banffshire, can now be added to that



## PROCEEDINGS

discovered in Perthshire in 1981—the first for the mainland of Scotland (*J. Conch., Lond.*, **31**, p. 135). All are on the same band of Precambrian (Dalradian) limestone. A full account of these important discoveries will be found on p. 388.

*Vertigo angustior* Jeffreys. This very rare snail has not previously been found alive in Wales. Jeffreys' type site (1830) was near Swansea, where he records finding only dead, possibly subfossil, shells. A full account of the two newly discovered populations in the Gower peninsula can be found in *J. Conch., Lond.*, **31**, p. 340.

*Leiostyla anglica* (Wood). The presence of this north-western species in Kent a century ago is of much interest. Unfortunately we have no record of the exact site, nor of the habitat (*Conchologists' Newsletter* no. 88: 154). Miss Fairbrass lived in Abbey Street, Faversham, and was a member of the Conchological Society from 1885 to her death in 1891.

*Boettgerilla pallens* Simroth. This introduced slug continues to spread, and during 1983 was recognised in six further vice-counties, including the first in Scotland.

*Perforatella rubiginosa* (Schmidt). First discovered in Britain only in 1982 (*J. Conch., Lond.* **31**, p. 201; *London Naturalist* no. 62: 59), this species can now be recorded from two further sites along the Thames. The specimens from Pangbourne were identified by the late Dr. Quick as *Trichia 'liberta'* (= *plebeia*) (*J. Conch., Lond.*, **24**, p. 397) but their shell characters are those of *P. rubiginosa*. The Pangbourne site is apparently now destroyed.

*Hygromia cinctella* (Draparnaud). This common Mediterranean helcid is now well established over a considerable area in South Devon, but has not hitherto been found elsewhere in southern England. The Dorset population is in urban waste ground.

*Helicigona lapicida* (L.). The new site in Carmarthen represents a considerable westward extension of the known range of this species in Britain. At Dryslwyn Castle it survives precariously on two short stretches of unrestored walling; most of the ruin has been tidied up and repointed by the Ministry of Works and *H. lapicida* is absent.

M. P. KERNEY

## RECORDER'S REPORT: MARINE MOLLUSCA

Since publication of the *Marine Atlas* in 1982, many new records have been provided which will be published as additions and amendments in a forthcoming paper in *Journal of Conchology*. Of particular interest are the following:

*Lepidopleurus scabridus* (Jeffreys). This chiton is restricted to the west Channel, and the Atlas shows only pre-1951 records. It was collected alive in the Channel Islands (S 17) in 1980 by A. Stiva (*C. B. van de Ned. Mal. Ver.*, No. 207 (1982), p. 1279).

*Acmaea testudinalis* (Müller). This northern species (southern limit according to the Atlas is Yorkshire–N. Wales) occurs at several stations just south of the Channel Islands, within the French sector of sea area S 17. (Retiere, *Contribution a la Connaissance des Peuplements Benthiques du Golfe Normanno-Breton*, 84 (1979) Thesis, University of Rennes).

*Caecum clarkii* Carpenter. This species, new to the British Isles, has been found in the Channel Islands (S 17). D. F. Hoeksema found a shell with periostracum in 1979 (*Basteria*, **45** (1981), p. 66) and A. Stiva collected a fresh shell with dried remains and operculum, together with more empty shells, in 1982. (*C. B. van de Ned. Mal. Ver.*, No. 210 (1983), p. 1333). The Caecidae are reviewed by van Aartsen in *Basteria*, **41** (1977), p. 7.

*Philinoglossa praelongata* Salvini-Plawen. This animal has been found by L. v. Salvini-Plawen in Plymouth Sound in 1982, the first record outside the Mediterranean (*J. mar. biol. Ass. U.K.*, **64** (1984), p. 497).

*Cuthona genovae* (O'Donoghue). This Mediterranean species was found in Lough Hyne (sea area S 37) in 1980 and 1981, its first record for the Atlas area (Wilson and Picton. *Ir. Nat. J.*, **21** (1983), p. 69; *J. Conch. Lond.*, **31** (1984), p. 349).

The following changes in Area Representatives have taken place:

S 1 SHETLAND Dr. J. D. Peacock has resigned and Mr. A. Skene has agreed to act for it as well as for his existing area S 3 Orkney.

S 10 DOGGER Mr. J. Llewellyn-Jones has handed over to Mr. T. Pain of 47, Reynolds House, Millbank, London, SW1P 4HP.

S 14 EAST CHANNEL Mrs. C. J. Pain has resigned and the Area will be represented by the previous Marine Recorder, Mr. C. P. Palmer, 9, Upton Dene, Grange Road, Sutton, Surrey, SM2 6TA.

I thank the retiring representatives for their efforts, help and advice, particularly in the Atlas preparation, and am glad that their areas will remain in good hands.

S 29a ANTRIM Mr. M. Brisco has moved to a new address: c/o John Innes Institute, Colney Lane, Norwich.

S 16 PORTLAND and MARINE RECORDER I also have moved and correspondence should be addressed to: Barn Court, Hamlet, Chetnole, Sherborne, Dorset, DT9 6 NY.

D. R. SEAWARD



## COMMUNICATIONS

### *PTYCHOTREMA WALIKALENSE* PILSBRY NEW TO EAST AFRICA

Whilst sorting through a drawer full of specimens at the British Museum (Nat. Hist.) to which H. B. Preston had given manuscript names, a box containing two rather worn specimens of the above species was found mixed with them. The box bears a pencilled label in M. Connolly's handwriting 'walikalense Pilsbry Kayonsa For. Kigezi 7200'. It is well known that Connolly bought up a large collection of African snails from Preston most of which had been given names which had never been published and, although Connolly published many of them, some hundreds remained and were given to the Museum together with other material. This present lot has no connection with Preston and although no collector is mentioned I feel fairly certain that it was probably C. R. S. Pitman, who collected a very considerable number of specimens now scattered in many museums but whose collection was never dealt with as a whole. By some oversight the specimens of *P. walikalense* were never placed in the general collection and thus overlooked. The record may be formally stated as follows.

*Ptychotrema walikalense* Pilsbry in *Bull. Am. Mus. Nat. Hist.* **40**, p. 203, Fig. 72 (1919).

UGANDA. Kigezi District, Kayonsa Forest, 2160 m prob. leg. C. R. S. Pitman (Brit. Mus. (Nat. Hist.)).

Also present were two small lots collected in the Mabira Forest (Uganda, 1140 m.) by Pitman comprising *Gulella pupa* (Thiele), *G. disseminata* (Preston), *G. sellae* (Pollonera) and *G. lessensis* Pilsbry.

B. VERDCOURT,  
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### *VERTIGO ALPESTRIS* ALDER IN SCOTLAND

This communication describes two new records for *Vertigo alpestris* Alder in Scotland and adds notes on the only two previous records.

On 7 July 1983 we revisited the site in Glen Tilt, Perthshire where we had found a single specimen of *V. alpestris* in 1981 (*J. Conch.*, *Lond.* (1983) **31**, p. 135). We found several more live and dead specimens on scree 200–300 m to the north of the original site. The new sites were large areas of limestone scree at a low angle. Unlike the original site there was moss growing on the scree: *Ditrichum flexicaule* Hampe, *Tortella tortuosa* (Hedw.) Limpr. and *Hypnum compressiforme* L. There were few higher plants growing in the scree except some *Mercurialis perennis* L. and *Geranium robertianum* L. This new area is a more typical site as the *V. alpestris* were easier to find and is very similar to the two new sites described below.

In May 1983 four dead shells of *V. alpestris* were found in debris collected on 6 June 1982 in Glen Builg, Banffshire. On 27 August 1983 live specimens of *V. alpestris* were found at two other sites in Glen Builg (NJ186051 and NJ181064). All three sites were limestone scree facing west or south-west at an altitude of 425 m. Fossil *V. alpestris* have recently been found in an early Flandrian tufa in Glen Builg (*Scott. J. Geol.* (1984), in press) suggesting that this species has a long history of occurrence in this area. The limestone boulders where the specimens were found had the mosses *Ditrichum flexicaule* and *Tortella tortuosa* growing on them. *Mercurialis perennis*, *Rubus idaeus* L., *Urtica dioica* L., *Geranium robertianum*, *Polystichum lonchitis* (L.) Roth, *Asplenium viride* Hudson and *A. trichomanes* L. grew sparingly in the scree.

On 4 September 1983 we visited a third area of limestone scree at Craig Leek, Aberdeenshire (NO 189928), 12 km due south of the Glen Builg sites, and found several live specimens of *V. alpestris*. This low-angled scree faced south-east at an altitude of 400 m. It was very similar to the previous sites being stable scree with lichens and the mosses *Ditrichum flexicaule*, *Tortella tortuosa* and *Racomitrium lanuginosum* (Hedw.) Brid. growing on the boulders. The sparse growth of higher plants included *Mercurialis perennis*, *Urtica dioica*, *Geranium robertianum* and *Asplenium trichomanes*.

All three localities described are on the same band of Dalradian limestone that stretches from Schiehallion in Perthshire to Tomintoul and beyond in Banffshire. The specimens of *V. alpestris* were located usually among moss growing on boulders that were part of stable scree. No other molluscs were found in immediate association although calcicolous species such as *Ena obscura*, *Lauria cylindracea*, *Arianta arbustorum* and *Clausilia bidentata* were found in the scree and the areas round about were rich in molluscs.

The only other Scottish record for *V. alpestris* is from Mull, Inner Hebrides, in 1948 (*J. Conch.*, *Lond.* (1949) **23**, pp. 41–42). On 24 and 25 September 1983 we visited the Tobermory area and searched the area described by the finder,



## COMMUNICATIONS

L. B. Langmead. In particular we tried to find the natural site described by him for *V. alpestris* 'some large boulders lying in the open and standing some 6 to 8 feet high' (loc. cit.). While the north and west end of the wood appears to be similar to what Langmead described, the south and east end now has *Rhododendron ponticum* L. scrub invading and has coniferous afforestation. We eventually found what we thought were the boulders described above (though we cannot be absolutely certain as the description is not that clear). They are now more-or-less covered in *Rhododendron ponticum*, and we failed to find *V. alpestris*. Most boulders and the stone walls, being generally overhung by trees, and covered very thickly with moss, looked unsuitable for *V. alpestris* by comparison with the other Scottish sites. We also failed to locate *Balea perversa* on the wall, where Langmead found it. It is interesting that he describes the boulders where he found *V. alpestris* as 'lying in the open' and the only plants on them that he mentions were 'a few meagre rosette Compositae'. It would seem likely that this first Scottish site for *V. alpestris* is no longer suitable and the species is extinct there. This is a great pity as it would have made an interesting comparison with the other three localities.

We should like to thank Dr. M. P. Kerney for confirming the identification of *V. alpestris* specimens and Mr. A. G. Payne for identification of the mosses.

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ANNOUNCEMENT

ICSEB-III

THIRD INTERNATIONAL CONGRESS OF SYSTEMATIC AND  
EVOLUTIONARY BIOLOGY, 1985

The Congress will be held on 4–10 July 1985 at the University of Sussex, near Brighton, England.

The following Congress Symposia are being organised:

- Symbiosis in Evolution
- Conservation of Tropical Ecosystems
- Biogeographic Evolution of the Malay Archipelago
- Adaptational Aspects of Physiological Processes
- Co-evolution in Ecosystems and the Red Queen Hypothesis
- Angiosperm Origins and the Biological Consequences
- The Measurement of Rates of Evolution
- Molecular Biology and Evolutionary Theory
- Co-Evolution and Systematics
- Molecules vs. Morphology in Phylogeny: Conflict or Compromise?
- Random and Directed Events in Evolution
- Biochemical Innovation in Microbial Communities

There will also be Special Interest Symposia on other topics, as well as sessions for contributed papers, films and poster papers.

**For further information write to: Professor Barry Cox  
ICSEB Congress Office  
130 Queen's Road,  
Brighton,  
Sussex BN1 3WE, UK.**



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